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BROWN STAIN IN PINE SAPWOOD CAUSED BY *CYTOSPORA* SP.[1]

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Abstract

A fungus isolated from naturally brown-stained red pine sapwood was found to produce characteristic chocolate brown stain in sterilized red pine sapwood in culture; it is identified as a species of *Cytospora*. The fungus develops in the ray parenchyma, may proliferate in the tracheids, but penetrates the walls only through the pits. A technique is described for producing brown stain in culture in sticks of the size required for static bending and toughness tests. Two series of sticks were subjected to each test; the samples used were end-matched sticks in groups of three, which provided a green control, sterilized control, and specimen stained in culture by *Cytospora* sp. The results showed some variation in the relative strength of samples in different groups, but a statistical analysis indicated that the effect of *Cytospora* sp. on both bending strength and toughness is negligible.

A chocolate brown stain frequently develops in the sapwood of red pine (*Pinus resinosa* Ait.) and jack pine (*P. Banksiana* Lamb.) logs and poles in Eastern Canada during storage; it has also occasionally been found in eastern white pine (*P. Strobus* L.). Hubert (1) reports its common occurrence in red pine and jack pine in the Lake States, and in western yellow pine (*P. ponderosa* Laws.) in the western United States and in British Columbia; he also noted its occasional development in western white pine (*P. Monticola* Dougl.), sugar pine (*P. lambertiana* Dougl.), and pinon pine (*P. monophylla*). Thus it has a fairly general distribution in the pines, but appears to develop most vigorously in species of the hard pine group.

This stain has been reported for many years among sapwood stains of fungal origin, but no previous attempt has been made to isolate and identify the organism responsible for the discoloration or to determine its effect on the strength of wood.

Part 1. Cause and Development of Brown Stain

A. ORIGIN OF STUDY

Chocolate brown stain is so conspicuous and unsightly (Figs. 1A, 1B) that in recent years the users of pine poles have become increasingly concerned as to its cause and its effect on the mechanical properties of wood; serious

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Contribution from the Forest Products Laboratories Division, Department of Resources and Development, Ottawa, Ont.

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monetary loss has occurred owing to rejection of poles affected with this stain. In 1947 nine red pine poles were received at the Forest Products Laboratory, Ottawa, Canada, for study; they had been graded by the sender as containing light, medium, and heavy brown stain. The poles were tested for strength and samples obtained for pathological study. On examination it was noted that the sapwood presented a mottled appearance, showing various paler discolorations mingled with blue and chocolate brown.

Mechanical tests indicated that variation in strength did not correspond with the intensity or distribution of the brown discoloration. Cultures made from the sapwood yielded a fungus which produced a brown mat on malt agar and stained the medium an intense dark brown to black; other cultures contained fungi of the type associated with wood rots. Since in these poles no correlation had been shown between brown stain and loss of strength, and since the sapwood contained a mixture of fungi, it was necessary to reduce the variable factors under test, and to start our study with a laboratory investigation of brown stain alone.

B. Identification of Causal Fungus

The quite consistent isolation from brown-stained areas in the wood of the brown fungus mentioned above immediately suggested that it might be responsible for the production of the discoloration in the wood. Sterilized chips of red pine sapwood were, therefore, placed on mats of the fungus grown on malt agar in Petri dishes; these became infected in a few days and soon showed the characteristic brown discoloration. Sterilized sticks ($5\frac{1}{4}$ in. $\times$ 1 in. $\times$ $\frac{3}{8}$ in.) were later inoculated under aseptic conditions and incubated at 27° C. until good growth was obtained. It was found that the fungus readily penetrated the wood and stained it as in the previous test; the fungus was then re-isolated on malt agar, on which it produced mats similar to those originally obtained from the naturally stained wood. These tests established this fungus as the cause of chocolate brown sapwood stain.

After a few weeks growth on red pine sapwood blocks in culture the fungus produced small nodules on the surface. Microscopic study showed that these were fertile pycnidia typical of the genus *Cytospora*. The fungus is, therefore, identified as *Cytospora* sp.

C. *Cytospora*

As far as can be ascertained this is the first record of a *Cytospora* on any of the pines in the wood of which this stain has been observed; it is also the first record of a *Cytospora* causing sapwood stain.

The genus *Cytospora* has a widespread distribution and contains some two hundred species. Until the genus is monographed it seems fruitless to attempt a specific identification of our isolate; it is very probable that it should be described as a new species. An attempt will be made by growing the fungus on different media to induce the development of the perfect stage of fructification.

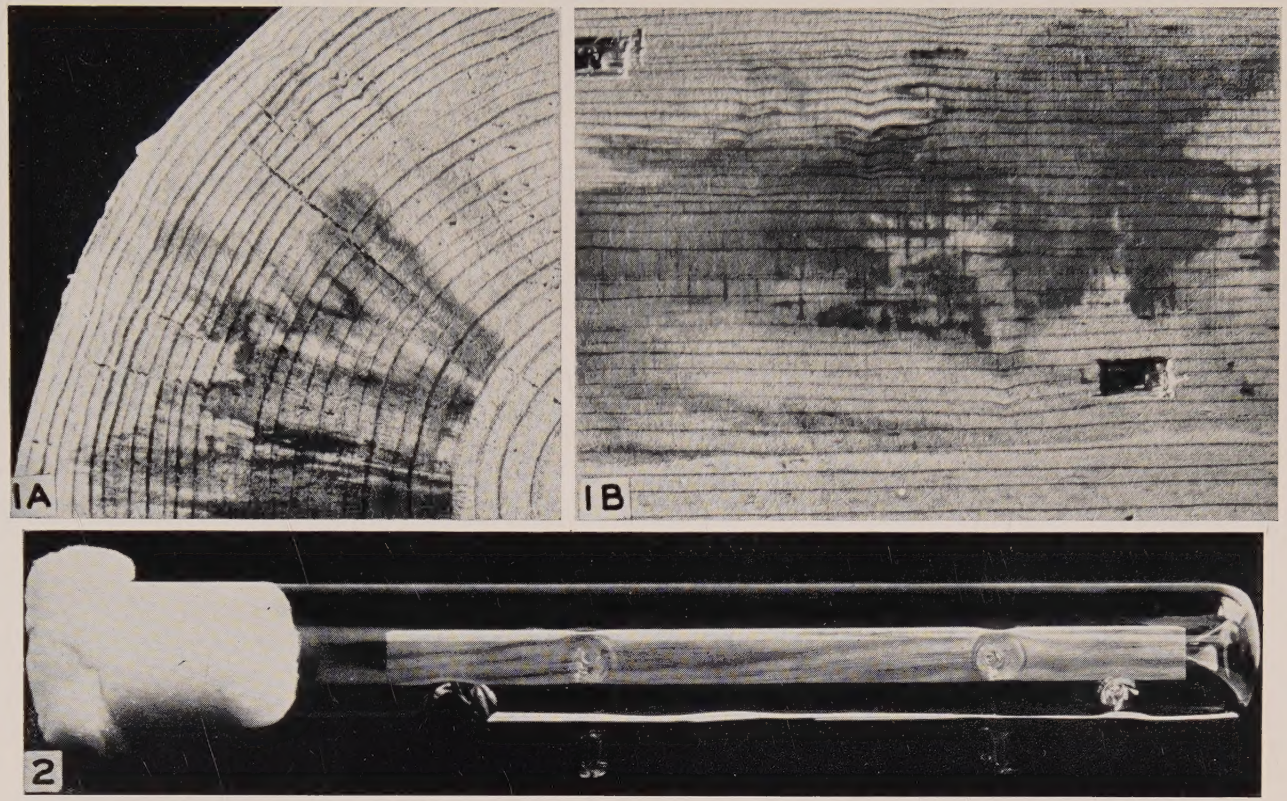
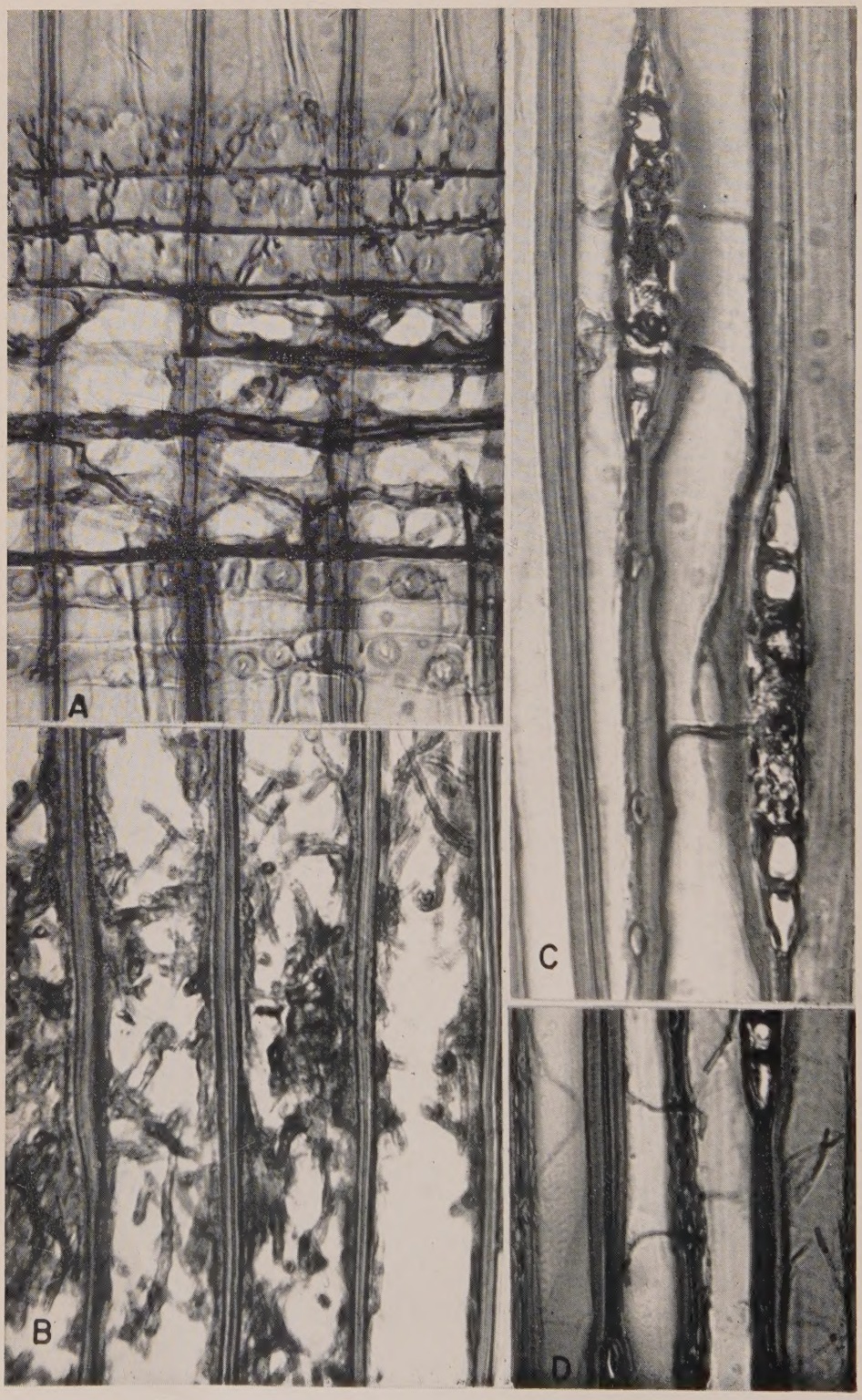


FIG. 1. Brown stain in red pine sapwood: A—transverse face; B—longitudinal face.
FIG. 2. Red pine sapwood test stick in culture tube.


A
B
C
D

a. Malt Agar Cultures

The fungus grows well on malt agar; from a centrally placed inoculum it covers a plate 9 cm. in diameter in six days. The mat is at first colorless and filmy with even margin and a slightly fuzzy surface; brown color shows up first in the older growth around the center and gradually extends toward the periphery in radiating lines. Finally the whole mat becomes dark brown, and the agar is stained deep brown to black. The surface growth thickens somewhat, and pycnidial initials develop sparsely (more abundantly in tube than in plate culture); but fertile pycnidia have not been observed on agar.

b. Wood Cultures

Preliminary tests indicated that *Cytospora* sp. will penetrate wood of quite varied moisture content. Sterilization of green red pine sapwood removed considerable water, giving a range of moisture content, as determined from sample sticks, of 95% to 115%. Growth of the fungus was good on such material; sterilized green sapwood of moisture content throughout the natural range obtained after sterilization was therefore used in this study.

(*a*) *Staining*

Sticks inoculated and incubated as discussed below were stained a uniform chocolate brown in three months. Microscopic examination revealed that the discoloration is caused chiefly by a deep yellow-brown staining of the cell walls; brown fungal hyphae are fairly abundant, but much of the mycelium in the wood is hyaline.

(*b*) *Hyphal Penetration*

Examination of microscopic sections shows that the fungus develops in the ray parenchyma (Fig. 3A), often entirely destroying the cells, and consuming the food reserves stored therein. The hyphae pass through the wood in a characteristic manner. At the ray crossings, branches from the mycelium in a ray pass through the thin walls of parenchyma cells, and the windowlike pits in the walls of adjacent tracheids, to reach the lumina of those tracheids (Fig. 3C). Here they may branch to form a considerable mass (Fig. 3B), or without excessive proliferation may extend longitudinally and send branches into neighboring rays to attack the parenchyma there. No boring through tracheid walls has been noted; the fungus may pass directly from tracheid to tracheid, but, as far as has been observed, such penetration is always through bordered pits (Fig. 3D). This failure to puncture the walls probably accounts for the fact that, as shown below, the fungus does not affect the strength properties of the wood. The mycelium is more abundant in the springwood than in the summerwood.

(*c*) *Pycnidia*

Good pycnidial development was obtained on wood blocks five weeks after inoculation. The valsoid stroma forms in superficial cushions with

FIG. 3. Hyphae of *Cytospora* sp.: A—in ray parenchyma cells, ×450; B—massed in tracheids, ×450; C—passing from ray parenchyma cells to tracheid, ×580; D—passing through bordered pits in radial walls, ×380.

irregular chambers from which the spores are extruded in cirri. The spores are hyaline, slender allantoid, and measure 4 × 1 μ.

(*d*) *Production of Water*

In test series No. 2, discussed below, the inoculated sticks and sterilized controls were incubated for 13 weeks at 27° C. At the outset some free water was present in all the tubes. During the incubation period it was noted that the tubes containing control sticks tended to dry out somewhat, while in those in which the fungus was growing heavy condensation of water occurred on the inner walls. Since all the tubes were plugged and incubated in the same way, the escape of moisture would be more or less uniform in both sets; the condensed moisture was, therefore, due to an excess liberated by the fungus.

Cytospora sp. develops in the ray parenchyma, feeding on reserve substances which are rich in carbohydrates. In the breakdown of the latter to carbon dioxide and water a certain amount of heat is developed which would tend to force water out of the wood into the air of the tube, where it condenses on the slightly cooler glass walls. Since the final average moisture contents of the inoculated sticks (72.1% and 61.4%) were lower than those of the controls (84.2% and 88.1%) as recorded in Tables IV and V, the condensed water must have come at least in part from water originally present in the wood; but judging by the excess noted it would seem that this was augmented by an additional amount produced by the fungus. No pertinent weights have been recorded, so that it is not possible to determine the percentage due to fungal metabolism.

It is stated by men handling brown-stained poles that brown-stained wood is wetter than that not penetrated by the fungus. In poles, escape of water would be much less active than in small culture sticks with their proportionately large surface area. A considerable amount of the water liberated by the fungus would doubtless be trapped in the poles, either in the stained wood or in adjacent tissues. It is to be expected, therefore, that brown-stained sapwood would have a higher and less uniform moisture content than uninfected wood.

Part 2. Mechanical Tests

A. Technique

a. Inoculum

To determine the effect of brown stain on the mechanical properties of red pine sapwood it was decided to subject specimens to static bending and toughness tests, for which sticks measuring 2 cm. × 2 cm. × 32 cm. would be required. In order to stain sticks of this length uniformly, inoculum which can be distributed evenly over a longitudinal surface is required. Since spores of *Cytospora* are not readily obtained in culture, it was necessary to produce a suitable suspension of mycelium. To that end mats of the fungus were grown on malt agar in Petri dishes and minced in a Waring Blendor, all tests being conducted with sterilized apparatus under strictly aseptic conditions.

Mats grown on malt agar were removed from the plates under aseptic

conditions, with as little adhering agar as possible, and transferred to 100 cc. of sterilized distilled water in the jar of a Waring Blendor. They were minced for different periods of time to determine the effect of fragmentation on the viability of the fungus. Mincing for one minute gave a suspension sufficiently fine to be delivered by the pipettes used in transferring, and the viability of the mycelial fragments was excellent. Mats of different ages were then minced and tested, and it was decided that inoculum from a 10-day-old culture seemed most satisfactory. The standard inoculum adopted was, therefore, a suspension of a 10-day-old mat minced for one minute in 100 cc. sterilized distilled water.

b. Culture Tubes

Sticks 2 cm. × 2 cm. × 32 cm. are longer than those commonly used for culture work. It was, therefore, necessary to design a tube which would accommodate a stick of this size, hold it in a suitable position, and permit uniform inoculation over the length of one surface. Sticks placed in tubes held in an upright position tend to dry from the top, and uniform inoculation of an upright surface is difficult to achieve. It was decided to keep the sticks in a horizontal position with moisture below throughout the length of the stick, and to inoculate the upper longitudinal face. The tube design adopted is shown in Fig. 2; it measures 45 cm. in length and has an inside diameter of 6.4 cm.

The stick lies on two horizontal rests formed by indentations of the wall, the rest toward the mouth being closed across the tube to prevent free water from reaching the plug, and that at the closed end open to allow water to flow to the end of the tube. The stick is held in a central position and away from the end of the tube by indentations in the walls. It is necessary to have a tube 6.4 cm. in diameter in order to have space below to accommodate water freed from the wood during sterilization, and space above to permit the insertion of the long pipette used to apply inoculum over the length of the stick.

c. Check of Technique

After preliminary tests on sticks of the required size, a satisfactory technique seemed to have been developed; but before setting up a series for strength tests a final check was run. Three sticks, 2 cm. × 2 cm. × 32 cm., were cut and machined from green red pine sapwood oriented to provide longitudinal tangential faces for inoculation. Two strips of filter paper were placed one on top of the other along the lower wall of each tube between the rests on which the stick was to be placed; these were moistened with 5 cc. of distilled water to hold them in place, and to assist in maintaining a moist atmosphere. The sticks were laid in position with tangential face uppermost, the tubes plugged, and the assemblies sterilized for 30 min. at 15 lb. pressure.

The standard inoculum was introduced and spread over the upper face of each stick by means of pipettes which reached the length of the sticks. The plugs were covered with parafilm to prevent escape of moisture. The cultures thus prepared were incubated at 27° C.

The fungus grew readily over the surface of the sticks. After eight weeks one was removed and ripped; it was found that stain was quite well developed. The other two sticks were left in culture for an additional six weeks. Results indicated a period of 12 to 14 weeks as likely to provide for the development of stain satisfactory for test

B. Test Series No. 1

a. Material

A freshly felled log of red pine was obtained, and the sapwood converted to sticks for mechanical tests. Bark slabs were removed from two opposite sides of the log, and from each side a 5/4 in. board was sawn. These boards were then ripped into sticks 1 in. wide toward the center and 5/4 in. toward the periphery. The outer surface was dressed to give a tangential face and the sticks squared; all surfaces of each stick were dressed. After machining, the sticks measured 2 cm. × 2 cm. in cross section. Two bark slabs were removed from each side of the remainder of the log, and four 2 in. boards sawn and converted to sticks as described above. The sticks were then cut into 32 cm. lengths; 52 end-matched groups of three were obtained for strength tests, of which 29 were used in the static bending and 23 in the toughness test.

b. Procedure

The technique discussed above was followed. Two sticks of each group were sterilized in tubes, one was inoculated, and all were incubated at 27° C. The third stick was used as a green control and immediately subjected to the appropriate mechanical test.

Cytospora grew well and the sticks soon showed the characteristic brown discoloration. Owing to the appearance of a contaminating mold in some of the tubes after six to nine weeks' incubation, all the sticks were removed from the tubes in 9 to 11 weeks and immediately tested. The contamination developed on both inoculated sticks and uninoculated controls; since the latter had not been opened after sterilization it was evident that the mold had not been introduced during the manipulations of inoculation. It was found that the parafilm covering the plugs had trapped spores on their surface and also sealed in moisture which permitted germination; the hyphae then grew slowly through the cotton, sporulated on the inner surface of the plugs, and contaminated the sticks.

After the sticks were tested for strength, four cultures were made from each, two from each side of the load point. It was found that the contaminant had penetrated none of the inoculated sticks; pure cultures of *Cytospora* sp. were obtained from all the stained sticks; therefore, any change in strength properties of the brown-stained wood would be due to the action of *Cytospora* sp. alone. Of the 52 control sticks, however, 13 as indicated in Tables I and III yielded a growth of mold from beneath the surface. A mathematical examination of the results for strength of the contaminated control sticks in comparison with those for the clean controls showed that the mold had had

no effect on the mechanical properties under test. The results, therefore, may be accepted as if no contamination had occurred.

The inoculated sticks and controls were tested as soon as possible after removal from the tubes. After testing, a 3 in. piece was cut from one end of each stick for moisture content determinations; and, after cultures had been made as discussed above, the remaining portion was ripped in half to expose the stain which had developed.

c. Stain Development

Staining was complete in about half of the sticks, mottled and streaked in many, and marginal in the remainder. The variations are shown in Fig. 4A.

d. Results of Mechanical Tests

(a) Static Bending

The detailed results of these tests listed under fiber stress at proportional limit, modulus of rupture, and modulus of elasticity, are given in Table I, and

TABLE I

STATIC BENDING, SERIES 1

Stick No.	Moisture content, %		Sp. gr. (vol. at test-wt. oven-dry)		Fiber stress at proportional limit, p.s.i.		Modulus of rupture, p.s.i.		Modulus of elasticity, 1000 p.s.i.	
	Culture	Control	Culture	Control	Culture	Control	Culture	Control	Culture	Control
1*	64.8	98.4	.359	.363	2680	2680	5260	5160	723	723
2	75.6	82.4	.379	.413	2680	2790	5130	5020	716	646
3	70.7	77.6	.408	.430	2790	2750	5470	5470	786	768
4	70.8	74.1	.393	.451	2790	2790	5500	5430	761	769
5	89.1	84.1	.367	.393	2680	2680	5300	5230	781	747
6*	85.8	91.9	.370	.411	2620	2750	4810	5060	551	621
7	57.4	73.3	.414	.425	2720	2790	5810	5260	849	676
8	63.9	77.9	.416	.412	2720	2790	5400	4980	663	702
9	56.3	79.0	.393	.382	2790	2580	5540	4810	738	681
10	—	—	—	—	2680	2680	5570	4960	859	772
11	69.8	61.7	.429	.448	3110	3150	5600	5540	694	709
12	46.0	64.6	.424	.460	2520	2790	5540	5360	777	831
13*	62.1	72.8	.439	.421	3270	3270	6180	5430	827	795
14*	88.0	84.0	.405	.430	3150	3150	5480	5610	729	803
15*	55.2	64.6	.431	.435	3150	3190	5830	5870	811	849
16*	61.5	80.1	.411	.421	3400	3440	6060	5990	851	807
17	70.5	58.8	.383	.430	3350	2680	5770	5530	801	799
18	62.1	71.9	.374	.418	3190	2580	5580	4810	752	681
19	54.8	63.8	.407	.450	3230	3230	6420	5940	869	817
20*	79.8	73.4	.387	.384	3150	2520	5700	4940	742	692
21	44.5	64.8	.476	.468	2830	2720	6720	6120	746	764
22	59.3	62.4	.475	.493	3230	3270	6390	6730	601	719
23	47.6	35.3	.481	.495	2580	2580	6460	6780	703	695
24	53.7	60.0	.454	.477	3230	3270	5970	6110	692	627
25*	72.5	72.1	.446	.400	2580	3230	5260	6230	703	675
26	68.4	71.6	.438	.436	3870	3150	6420	6020	838	820
27	65.8	75.7	.382	.404	3230	2580	5490	5200	690	687
28	57.0	56.2	.442	.494	3110	2580	5820	6040	567	726
29	37.3	29.4	.490	.501	2580	2580	6390	6420	641	660
Av.	63.9	70.1	.417	.434	2960	2870	5750	5590	740	733

* *Controls contaminated.*

TABLE II

STATIC BENDING, SERIES 2

Stick No.	Moisture content, %		Sp. gr. (vol. at test-wt. oven-dry)		Fiber stress at proportional limit, p.s.i.		Modulus of rupture, p.s.i.		Modulus of elasticity, 1000 p.s.i.	
	Culture	Control	Culture	Control	Culture	Control	Culture	Control	Culture	Control
1	70.5	71.5	.385	.448	2270	2630	5030	5410	843	926
2	93.4	72.1	.373	.436	2310	2340	5320	5670	931	963
3	72.7	96.0	.396	.404	1940	2000	4880	5180	998	959
4	76.7	95.2	.379	.416	1920	1950	5160	5050	913	916
5	85.6	65.9	.372	.436	2270	1950	4910	5020	957	899
6	81.6	96.5	.378	.398	2280	2290	5550	5500	959	1035
7	78.9	96.1	.372	.415	1950	2250	4310	4950	723	871
8	89.0	72.6	.369	.440	1920	2270	4770	5180	879	941
9	52.1	70.0	.417	.444	2270	2290	5760	5700	1002	1015
10	39.3	82.8	.439	.427	1930	1630	5480	5480	990	1031
11	64.8	75.0	.399	.445	2250	2290	5540	5610	1051	1053
12	59.2	86.8	.398	.426	2280	1960	5380	5650	916	1078
13	48.4	67.9	.408	.455	2870	2650	6850	6440	1138	1292
14	62.6	85.2	.389	.420	2920	2290	6350	6120	1067	1179
15	64.7	82.1	.385	.421	2610	1950	6190	5520	1138	1150
16	67.9	93.4	.377	.415	2260	2290	5920	6010	1002	1186
17	51.2	85.0	.434	.415	2280	2270	5470	5610	1064	1082
18	76.3	99.2	.394	.415	2260	1610	5570	5100	1034	1013
19	86.3	103.6	.362	.404	2610	1950	5340	4970	916	914
20	82.8	101.5	.339	.371	1940	2000	4750	4350	829	850
21	74.1	72.0	.372	.436	2250	1950	5540	5630	942	1008
22	96.3	75.7	.348	.428	2560	1980	5360	5460	893	1027
23	83.4	89.4	.382	.410	1950	1610	5240	5080	967	988
Av.	72.1	84.2	.386	.423	2270	2100	5420	5420	963	1016

the average figures together with those for the green controls in Table IV. Sterilization caused a reduction of all the strength properties; but for the present study the pertinent comparison is between the sterilized inoculated sticks and their sterilized controls, since for these the only variable was the presence of the brown-staining fungus.

Considerable variation in the samples will be found in the tables in the results obtained for all the properties tested. As regards fiber stress at proportional limit, it will be seen that, of the 29 samples tested, 11 were lower than, 9 equal to, and 9 higher than their sterilized controls; in modulus of rupture, 19 showed greater strength than their respective controls; and stiffness, as determined by modulus of elasticity, was higher than the controls in 17 samples. Sticks showing variations in intensity and distribution of stain did not show any regularity in strength properties. Those with complete and intense stain fell into all groups: lower than, equal to, and higher than their controls; and the same was true for those containing mottled or marginal discoloration.

TABLE III

TOUGHNESS

Series 1							Series 2						
Stick No.	Moisture content, %		Sp. gr. (vol. at test-wt. oven-dry)		Toughness in-lb.		Stick No.	Moisture content, %		Sp. gr. (vol. at test-wt. oven-dry)		Toughness in-lb.	
	Culture	Control	Culture	Control	Culture	Control		Culture	Control	Culture	Control	Culture	Control
1	76.5	81.2	.390	.418	472.2	353.6	1	78.5	101.9	.376	.407	392	274
2	55.8	80.0	.420	.402	373.0	434.9	2	93.6	91.8	.349	.394	287	254
3*	74.4	84.3	.369	.403	409.1	458.5	3	80.0	106.4	.352	.377	201	248
4*	44.8	91.1	.393	.378	483.3	473.4	4	62.6	91.5	.396	.429	240	259
5	60.6	84.9	.389	.409	486.5	441.7	5	69.8	99.8	.409	.402	260	245
6	55.5	79.5	.402	.433	399.1	409.1	6	35.8	78.8	.408	.423	247	248
7	62.2	71.8	.390	.445	295.2	368.6	7	50.5	90.4	.419	.424	260	245
8	72.8	70.1	.365	.409	402.0	298.6	8	80.2	86.3	.386	.409	279	269
9*	59.1	76.2	.385	.386	411.8	181.3	9	45.0	79.8	.426	.443	242	242
10	56.5	81.0	.360	.421	378.9	290.4	10	47.4	84.7	.411	.432	275	289
11	60.8	85.5	.397	.438	515.4	478.4	11	47.0	71.1	.421	.443	252	295
12*	58.4	83.8	.430	.397	514.4	395.0	12	60.1	88.8	.403	.418	279	295
13	65.7	75.7	.422	.423	521.0	462.3	13	42.8	86.1	.408	.397	240	260
14	62.9	67.4	.395	.416	446.9	462.3	14	58.9	87.2	.378	.409	221	257
15	57.1	66.6	.407	.430	480.9	525.3	15	63.3	90.6	.382	.395	250	231
16	39.2	69.9	.460	.447	518.8	546.9	16	46.5	93.1	.388	.405	238	243
17	90.6	90.2	.371	.395	402.0	395.0	17	55.7	93.5	.385	.387	287	198
18	41.9	62.8	.461	.472	509.9	295.2	18	55.3	95.5	.391	.405	247	226
19	42.9	59.5	.465	.482	278.8	553.8	19	63.1	94.8	.365	.400	208	247
20	54.5	51.9	.462	.480	440.3	498.6	20	71.8	100.0	.363	.377	217	199
21	45.5	61.5	.452	.452	402.0	468.5	21	69.9	93.9	.372	.400	210	219
22	61.0	75.0	.406	.419	503.2	489.2	22	65.1	70.8	.389	.437	284	274
23*	65.2	72.0	.403	.415	449.5	262.1	23	66.4	66.7	.385	.457	245	287
							24	63.5	70.1	.391	.413	208	238
Av.	59.3	74.9	.408	.425	438.9	414.9		61.4	88.1	.390	.412	253	252

**Controls contaminated.*

(*b*) *Toughness*

The results in this test follow the pattern of those obtained for static bending. Of the 23 samples tested, 13 were higher in toughness, and 10 lower than the corresponding sterilized controls (Table III); and, as in static bending, toughness was not correlated with distribution of stain in the samples.

It is to be noted that the specific gravity of the stained sticks is lower than that of the sterilized controls.

e. Analysis of Results

A statistical analysis of the results presented in Tables I and III showed that the differences indicated by the arithmetical means are not significant. This analysis reveals that the effect of brown stain caused by *Cytospora* sp. on the mechanical properties of red pine sapwood in these tests was negligible.

C. Test Series No. 2

a. Material

The test samples were prepared from a freshly felled log of red pine which had been quartered before delivery. Two adjacent quarters provided sufficient sapwood for the tests; these were each sawn into two equal lengths and the four pieces converted to sticks of the same size and orientation as those used in series No. 1.

Twenty-three end-matched groups of three were used for the static bending and 24 for the toughness test.

b. Procedure

The technique adopted for series No. 1 was followed except that the plugs were left uncovered. The green controls were subjected to mechanical test immediately after they were machined; the sterilized controls and inoculated samples were incubated for 13 weeks at 27° C. and then immediately tested on removal from the tubes.

No contamination was visible in any of the tubes during the incubation period, but a check was made by culturing from the samples as in series No. 1. It was found that no contamination had occurred in any tube.

Moisture content was determined and the sticks ripped to expose internal stain as in the previous test.

c. Staining

At the conclusion of the incubation period the sticks were similar in external appearance to those in the first series. Internally, all except four of the sticks were stained a quite uniform more or less chocolate brown, with only occasional light flecks or narrow streaks; the four exceptions were light buff in color; the two types and a control are shown in Fig. 4B. Mycelium was present throughout the sticks, but less abundant in those not deeply stained.

TABLE IV

Static bending

(Average figures)

Series	Condition	Moisture content, %	Sp. gr. (vol. at test-wt. oven-dry)	Fiber stress at proportional limit, p.s.i.	Modulus of rupture, p.s.i.	Modulus of elasticity, 1000 p.s.i.
1	Green controls	107.4	.439	3360	6200	812
	Sterilized controls	70.1	.434	2870	5590	733
	Stained samples	63.9	.417	2960	5750	740
2	Green controls	172.4	.406	2670	5870	1051
	Sterilized controls	84.2	.423	2100	5420	1016
	Stained samples	72.1	.386	2270	5420	963

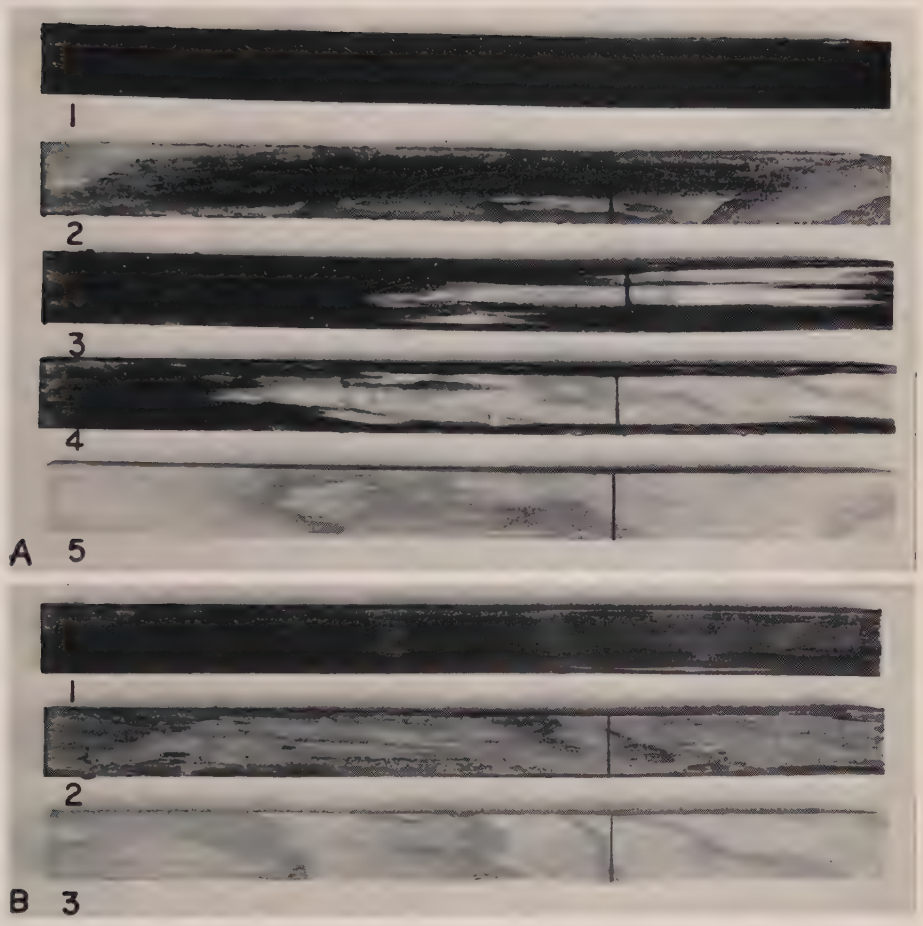


FIG. 4. Test sticks showing variations in stain: A—Series 1, 1–4 stained, 5 control; B—1 and 2 stained, 3 control.

TABLE V

TOUGHNESS

(Average figures)

Condition	Series 1			Series 2		
	Moisture control, %	Sp. gr. (vol. at test-wt. oven-dry)	Toughness, in-lb.	Moisture control, %	Sp. gr. (vol. at test-wt. oven-dry)	Toughness, in-lb.
Green controls	122.5	.424	464.6	174.1	.412	261
Sterilized controls	74.9	.425	414.9	88.1	.412	252
Stained samples	59.3	.408	438.9	61.4	.390	253

d. Results of Mechanical Tests

The detailed results of the static bending test are presented in Table II, and of the toughness test in Table III; average figures will be found in Tables IV and V. The results obtained agree with those of series No. 1; considerable variation will be found in the results obtained for the different samples in all the properties recorded, but the average figures indicate that there is no significant difference in the strength of the stained sticks and their sterilized controls.

Conclusions

It has been shown that a species of *Cytospora* causes chocolate brown stain in the sapwood of red pine and jack pine poles held under unfavorable storage conditions. The fungus develops in the ray parenchyma, stains the cell walls, but penetrates the walls only through the pits. Mechanical tests carried out on sticks stained in pure culture showed that the effect of the fungus on bending strength and toughness is negligible.

Acknowledgments

The writer wishes to acknowledge her indebtedness to Mr. W. E. Wakefield, Chief, Timber Mechanics Section, Forest Products Laboratory, Ottawa, for arranging for the machining of test samples, and the carrying out of mechanical tests; and to Miss E. I. Kennedy, Statistician, Timber Mechanics Section, for the mathematical evaluation of results.

Reference

1. HUBERT, E. E. Sap stains of wood and their prevention. U.S. Dept. Commerce, National Committee on Wood Utilization. 1929.

OBSERVATIONS ON AMYLOLYTIC BACTERIA

III. CULTURAL CONDITIONS INFLUENCING THE BREAKDOWN OF STARCH BY STENOTHERMOPHILIC BACTERIA BELONGING TO *BACILLUS STEAROTHERMOPHILUS*[1]

By Egon Stark[2] and P. A. Tetrault[3]

Abstract

Thirty-five cultures of *Bacillus stearothermophilus* hydrolyzed five starches under various cultural conditions. Hydrolysis occurred regardless of the type, brand, or batch of starch; regardless of the initial pH or of the subsequent pH changes of the medium. Starch in broth was better attacked than in agar media. Some cultures hydrolyzed 0.5%, but not 1% starch; others hydrolyzed easily 10% soluble starch. Length of incubation was important. Certain cultures never formed acid or sugar from starch. Dextrinization was a more reliable indication of starch hydrolysis than was the formation of acid or sugar. Soluble starch gave more consistent results in repeated experiments than did nonsoluble starches. The type of protein medium determines strongly the formation of amylase. Trypticase was the best commercial medium, yeast extract came second. The other 10 media yielded fewer amylolytic cultures. Yeast extract added to media enhanced amylase formation, except with trypticase. Tryptose, proteose-peptone, and neopeptone inhibited the growth of most cultures.

Introduction

There exist over 1000 references in the literature describing the breakdown of starch by bacteria, but only some 75 mention it in the title. Most of the papers dealt with mesophilic cultures. Gaughran (5) mentioned 12 investigators who observed the breakdown of starch by thermophilic bacteria. Stark (11) listed 18 additional references. The hydrolysis of starch was only one of many characteristics used to describe the organisms. The only serious attempts to study the action of thermophilic bacteria on starch were made by Coolhaas (3), by Imsenecki and his associates (7, 8), and by Proskuryakov and Dimitrievskaya (10).

Coolhaas studied the changes of the medium produced by the cells of bacteria. *Bacillus thermobutyricus*, one of the two species described by him, produced gas from carbohydrates. This led Gaughran (5) to believe that the culture was mixed.*

Imsenecki was the first to obtain cell-free amylase from the medium at 60° C. using *Bacillus diastaticus* Boyarska. Imsenecki, Solntzewa, and Kuzyurina (8) and Imsenecki and Solntzewa (7) described cultural conditions as well as the activity of the amylase.

[1] *Manuscript received January 2, 1952.*

Contribution from the Laboratories of Bacteriology, Department of Biological Sciences, Purdue University, Lafayette, Ind. Part Two of a thesis submitted by the senior author to the Graduate School of Purdue University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Presented before the 51st General Meeting of the Society of American Bacteriologists, Chicago, Ill. 1951. Abstracted in Bact. Proc. 1951. p. 27.

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* *Gaughran stated that Bacillus thermoamylolyticus produced gas from carbohydrates. In Bergey's Manual of Determinative Bacteriology, B. thermoamylolyticus is described as forming acid and gas from several carbohydrates, while B. thermobutyricus is not even mentioned by name. The original description by Coolhaas mentioned the formation of gas from several carbohydrates by B. thermobutyricus only. B. thermoamylolyticus did not ferment carbohydrates except starch.*

Proskuryakov and Dimitrievskaya reported on the activity of cell-free amylase of a thermophilic variant of *Clostridium pasteurianum* cultivated at 55° C. or 60° C. This report is of interest because in Bergey's Manual of Determinative Bacteriology (2) this species is differentiated from *Clostridium butyricum* on the basis of its inability to hydrolyze starch.

The present paper describes the cultural conditions influencing the breakdown of starch by stenothermophilic bacteria, identified as belonging to *Bacillus stearothermophilus* (13). The hydrolysis of starch in the medium in the presence of the bacteria, rather than in the presence of cell-free amylase, was studied. The latter aspect of the problem is presented elsewhere (11). Specifically, the effect of starches from different plants (cereal or tuber) and from different manufacturers and distributors in the same protein medium, the effect of different protein media using the same starch, and the effect of various cultural conditions using the same starch and the same protein medium were investigated.

I. Effect of Different Starches

Broth cultures

Methods and Materials

The medium consisted of 1% trypticase, 0.5% yeast extract, and 0.5% of the respective starches. The inoculum was grown in a medium of the same composition, but without starch, for 20 hr. at 65° C. The trypticase–yeast extract medium was the same for all experiments, unless stated differently. One milliliter of the inoculum was removed aseptically and divided evenly between two tubes of starch broth. These were incubated at 65° C. for four days and were tested daily with $N/10$ iodine solution. The exact procedure for interpreting the results has been already described (12). The pH of the starch broth, when colorless with iodine solution, was measured with a glass electrode (Beckman model H2) and the presence of reducing sugars was tested with Fehling's solution. In cases where the starch iodine color persisted the experiment was stopped, nevertheless, after four days of incubation.

Results were expressed on the basis of samples and not on the basis of subsamples. Samples showing one subsample to be blue and the other to be violet, when tested with iodine solution, were called negative (amylase absent); those showing one subsample to be colorless, were called colorless despite the color of the other subsample. Differences in the intensity of enzymatic action between subsamples coming from the same inoculum were common. They were also observed in taxonomic studies (11, 13) with gelatin liquefaction, hydrogen sulphide formation, changes in litmus milk, and with other tests. New media for thermophilic bacteria are being developed in our laboratories in an attempt to make results more consistent.

The types and brands of starch tested are shown in Table I. With the first named brand two experiments were conducted, while the second brand and arrowroot starch were tested once only. These brands were used because they were readily available.

Results

The disappearance of the starch and the extent of the hydrolysis as shown by the iodine color and the formation of reducing sugars and of acids were the criteria used to evaluate results. These are summarized in Table I.

Formation of Reducing Sugars

No starch was saccharified by all 35 cultures. Soluble and potato starch, yielded the largest number of cultures forming reducing sugars. Rice starch on the contrary, yielded the lowest number. *B. stearothermophilus* ATCC 7954 and two other cultures formed sugar from all five starches. Two other cultures saccharified four starches, but not five.

Formation of Acids

No starch was acidified by all 35 cultures. The number of cultures acidifying soluble, potato, and arrowroot starches was surprisingly constant. Fewer cultures formed acid from rice and corn starch. Changes greater than 0.1 unit either way from the uninoculated control medium, pH 6.8, were called acidic or basic, respectively.

Disappearance of Starch

All cultures attacked all five starches, as shown by the conventional iodine test, under the conditions of the experiment. Soluble, potato and arrowroot starches were hydrolyzed by all 35 cultures within three days of incubation. Rice and corn starches, depending on the batch used, were hydrolyzed by all cultures in four days. However, in three instances, one or two cultures failed to attack the starch. The inoculum of these cultures showed only faint turbidity, indicating either poor growth or lysis.

(*a*) *Ease of hydrolysis*:—The number of amylolytic cultures not showing a blue color with iodine after one day of incubation was taken as an index of the ease with which a certain starch was attacked. The differences between batches and between brands of the same starch were quite large. However, the differences narrowed considerably upon prolonged incubation. Soluble starch was readily hydrolyzed. Potato and arrowroot starches resisted hydrolysis.

(*b*) *Extent of hydrolysis*:—The number of colorless cultures was taken as an index of the extent to which a particular starch was hydrolyzed. After the first day of incubation, the differences between batches and between brands of the same starch were again large. Potato starch offered the greatest resistance to complete hydrolysis.

(*c*) *Consistency of starch:*—The consistency of the starch after autoclaving differed from batch to batch. For example, nonsoluble starches formed sols which resisted dispersion despite vigorous shaking. In this case, not enough starch was left suspended to give a color with iodine; yet, the starch was visible on the bottom of the test tube or flask. This leads then to false positive results, indicating the complete hydrolysis of the starch (see Table I, corn

TABLE I

THE EFFECT OF COMMERCIAL STARCHES ON THE FORMATION OF AMYLASE BY STENOTHERMOPHILIC BACTERIA GROWN IN TRYPTICASE–YEAST EXTRACT BROTH AT 65° C.

Starch (type and brand)	Replication	Number of cultures									
		Iodine color								Acid pos.	Sugar pos.
		Not blue				Colorless					
		Days of incubation									
		1	2	3	4	1	2	3	4	4	4
Soluble starch											
City Chem. Co.	*a*	27	35	35	35	8	18	28	28	31	26
	b	30	34	35	35	16	25	26	26	31	24
Eimer and Amend	*c*	34	35	35	35	9	14	18	18	—*	—
Rice starch											
Coleman and Bell	*a*	21	32	34	35	17	20	24	24	17	6
	b	24	33	34	34	11	15	18	22	21	15
Cenco	*c*	13	27	30	33	8	10	16	19	—	—
Corn starch											
Baker and Adams	*a*	9	25	34	35	8	20	22	28	20	9
	b	25	31	33	34	25	25	27	27	24	20
Baker Chem. Co.	*c*	34	34	35	35	33**	25**	25**	18**	—	—
Potato starch											
Baker Chem. Co.	*a*	6	32	35	35	2	9	14	18	32	26
	b	26	34	35	35	7	10	12	12	32	23
Mallinckrodt	*c*	23	33	35	35	6	12	19	23	—	—
Arrowroot starch											
Baker Chem. Co.	*a*	19	34	35	35	6	9	16	19	31	21
	b	13	34	35	35	5	8	21	26	31	18

* *Not determined.*
** *Caused by false positive results.*

starch, Replication 6). Since the consistency of the starch is difficult to control, it is next to impossible to obtain identical results in repeated experiments.

Length of Incubation

The number of amylolytic and of colorless cultures increased with an increase in the period of incubation. Although stenothermophilic bacteria grew rapidly within three to four hours of incubation at 65° C., at least three days were required for all cultures to hydrolyze starch.

Strain Differences

Certain cultures never hydrolyzed starch to the colorless stage when tested with iodine solution. On the contrary, *B. stearothermophilus* ATCC 7954 always reached the achroöpoint within 24 hr. of incubation, regardless of the type, brand, or batch of starch used. Several other cultures, while not as rapid or as consistent as the known culture, also reached the colorless stage regardless of the starch. However, the fact that certain cultures hydrolyzed four, but not five starches completely, raises a complex problem concerning the physiology of bacteria and the properties of starch.

Agar Cultures

Methods and Materials

One test was conducted on a medium consisting of 1% trypticase, 0.5% yeast extract, and 2% agar. The medium was subdivided into five batches to which were added soluble, potato, corn, rice, and arrowroot starches, respectively, to give a final concentration of 0.5%. One loopful of a 48-hr.-old culture was used as inoculum. The plates were incubated for 48 hr. at 65° C. and the agar was then flooded with 0.1 *N* iodine solution.

Plates showing no zone of hydrolysis around the giant colony were treated as follows: the colony was scraped off with a spatula and the medium was again flooded with iodine solution. When held against transmitted light of a fluorescent office lamp any areas of clearing could be readily seen. Since this procedure is not convenient with agar slants, these become unsuitable for studies of this kind.

Another test was conducted on a nutrient agar–1% potato starch medium. The plates were incubated for 42 hr. at 65° C. before the agar was flooded with iodine solution.

Results

The results with 0.5% starch agar were surprisingly clear-cut: cultures forming a zone of hydrolysis around the colony on one starch did the same on all starches. Only *B. stearothermophilus* ATCC 7954 and six other cultures formed zones of clearing on starch agar. On soluble and rice starch these zones were visible to the eye without flooding. The other starches had to be flooded.

On nutrient potato starch agar better results were obtained: eight cultures (including *B. stearothermophilus* ATCC 7954) had a wide zone of clearing around the colony, seven cultures had a narrow zone, while 20 strains had no zone, but had cleared the starch below the colony. When plates were incubated only for 24 hr., 10 cultures showed a halo, while 25 cultures had cleared the starch only below their growth.

The formation of a zone on starch agar plates was a strain characteristic. The zones were formed within 24 hr. of incubation by the same cultures, on either 0.5 or 1% of potato starch.

For determinative work, starch agar plates are less useful than starch broth: many cultures which hydrolyzed 0.5% starch in broth did not show a halo of hydrolysis around the area of growth on 0.5% starch agar. However, starch agar plates are a valuable aid in the selection of potent amylase producing strains.

II. Effect of Different Proteins

Materials and Methods

The medium consisted of 1.5% of the respective protein and of 1% soluble starch. Media to which yeast extract was added consisted of 1% of the respective protein, 0.5% yeast extract, and 1% soluble starch. The yeast extract was included as a source of growth factors. The inoculum was grown in 1% trypticase – 0.5% yeast extract broth for 24 hr. at 65° C. Five-tenths of a milliliter were added to each tube containing 20 ml. of starch broth. The fermented medium was tested with iodine solution after one and four days of incubation. No acid or sugar determinations were made. Eight commercial protein media were used and are listed in Table II. All products were dehydrated Difco media, except Trypticase, manufactured by the Baltimore Biological Laboratories (BBL).

Results

Results are shown in Table II.

None of the media supported the formation of amylase by all 35 cultures tested. Trypticase without yeast extract was the best protein source. Yeast extract came second. All other media with or without yeast extract produced fewer amylolytic cultures. The addition of yeast extract to peptone, protone, tryptone, and tryptose enhanced the formation of amylase. When added to trypticase it had a depressing effect.

Neopeptone, proteose–peptone, and tryptose, in the concentration used, inhibited the growth of most cultures. The addition of yeast extract to tryptose alleviated the inhibitory effect somewhat. Yeast extract was not added to the other two media.

Not more than 10 of the 35 cultures hydrolyzed 1% of soluble starch to the colorless stage when tested with iodine solution within four days of incubation, regardless of the protein used. Since 28 cultures attacked 0.5% soluble

TABLE II

THE EFFECT OF COMMERCIAL PROTEIN MEDIA ON THE BREAKDOWN OF SOLUBLE STARCH BY 35 CULTURES OF STENOTHERMOPHILIC BACTERIA AT 65° C.

Medium	Number of cultures				
	Growth positive	Iodine color			
		Not blue		Colorless	
	Days of incubation				
	4	1	4	1	4
Peptone	35	20	24	4	9
Peptone and yeast extract	35	25	26	4	9
Protone	35	19	26	4	7
Protone and yeast extract	35	23	29	6	9
Tryptone	35	10	19	2	5
Tryptone and yeast extract	35	24	27	6	9
Trypticase	35	27	34	4	9
Trypticase and yeast extract	35	25	28	6	10
Tryptose	21	5	10	1	5
Tryptose and yeast extract	32	15	24	5	9
Yeast extract	35	27	31	4	10
Proteose–peptone	9	0	3	0	1
Neopeptone*	4	1	2	1	1

* *Only 25 cultures tested.*

starch to the colorless stage in the same medium (see Table I), the effect of the increased concentration of the starch upon certain cultures became very noticeable.

Length of incubation was again an important factor. Irrespective of the protein employed, more cultures hydrolyzed soluble starch after four days of incubation than after one day.

The above findings have far-reaching implications for taxonomic work. The indiscriminate use of protein media for identification tests may yield negative results for starch hydrolysis, despite the fact that the cultures are able to form amylase under better conditions.

III. Studies with Soluble Starch

1. *Effect of the Initial pH*

Using 0.5% soluble starch in 1% trypticase – 0.5% yeast extract broth, the initial pH was adjusted to 5.2, 6.0, 6.8, 8.0, and 9.0, respectively. Twenty milliliters of medium in a wide test tube were inoculated with 0.5 ml. of culture grown in 1% trypticase–0.5% yeast extract broth without starch at pH 6.8. Incubation was for four days at 65° C. Testing procedures were the same as described in the previous sections.

The extreme pH values of 5.2 and 9.0 inhibited the growth of most cultures. The three cultures growing at pH 5.2 attacked the starch well. Two of the four cultures growing at pH 9.0 hydrolyzed the starch within four days of incubation. These four cultures exhibited a lag period for growth extending over two days.

At pH 6, 7, and 8 all cultures grew rapidly and hydrolyzed starch.

Table III shows the effect of the initial pH of the medium on the breakdown of soluble starch at 65° C. by 35 cultures.

TABLE III

EFFECT OF INITIAL pH ON THE HYDROLYSIS OF SOLUBLE STARCH AT 65° C.

Criteria	Days incubated	Number of cultures		
		Initial pH		
		6.0	6.8	8.0
Amylolytic	1	33	30	26
Colorless	1	13	16	8
Colorless	4	23	26	35
Not acid	4	3	3	2
Fehling's pos.	4	28	24	22

After one day of incubation, an initial pH of 6.0 favored the hydrolysis of soluble starch more than did pH 6.8 or 8.0. Tests with cell-free amylase showed the optimum pH for saccharification and dextrinization of soluble starch was at pH 6.0. The number of amylolytic cultures decreased progressively as the initial pH increased.

After four days of incubation, starting at pH 8.0. all cultures reached the achroöpoint. This observation was of considerable significance because it revealed that all cultures were able to hydrolyze soluble starch to the colorless stage under favorable conditions. The number of colorless cultures decreased progressively as the initial pH decreased.

2. *pH Changes During the Fermentation of Soluble Starch*

The usual trypticase yeast extract medium containing 0.5% soluble starch was made up and 500 ml. aliquots were placed into 3-liter Fernbach flasks, giving a shallow layer of about 3/4 in. depth. The inoculum consisted of 10 ml. of a 24-hr.-old culture. Incubation was at 65° C. Every three hours, samples were aseptically removed and tested for their pH with a glass electrode. The experiment was conducted twice.

Three groups of cultures could be distinguished:

Group I formed acid consistently, the pH never going below 5.0. *B. stearothermophilus* ATCC 7954 and 24 other cultures belonged here.

Group II formed acid at first, never going below pH 6.0, then causing a reversal in the reaction of the medium. Seven cultures did this.

Group III consisted of three cultures which did not form any acid at all. Alkalinity increased steadily, reaching pH 8.4 in the most extreme case. Starch was hydrolyzed to the colorless stage as determined with iodine solution.

These findings constitute additional evidence that the formation of an acid reaction in starch broth is an unreliable criterion of the hydrolysis of starch. In cases where no acid is formed additional tests are required.

3. *Effect of the Starch Concentration*

Qualitative tests indicated that certain cultures were capable of hydrolyzing 10% soluble starch. The ability of *B. stearothermophilus* ATCC 7954 to saccharify various concentrations of soluble starch was studied quantitatively.

The culture was grown in 1% trypticase–0.5% yeast extract broth for 12 hr. at 65° C. Ten milliliters of the culture liquid were added to 300 ml. of 2% trypticase, 2% yeast extract broth contained in 3-liter Fernbach flasks. Soluble starch was added to give final concentrations of 0.5, 1, 2, 3, 5, and 10%, respectively. The moisture content of the air-dry starch was ignored. Incubation was for two days at 65° C. The amount of reducing substances formed, expressed as maltose, was measured by the method of Underkofler, Guymon, Raymon, and Fulmer (14). The uninoculated, but autoclaved starch media contained reducing substances. These were subtracted from the amount of reducing substances present in the fermented medium. Results, listed in Table IV, were expressed in per cent of the maximum theoretically possible amount of maltose, based on the relationship that 1000 parts of starch yield 1056 parts of maltose (1).

TABLE IV

SACCHARIFICATION OF DIFFERENT CONCENTRATIONS OF SOLUBLE STARCH IN THE MEDIUM OF *B. stearothermophilis* AT 65° C.

(Per cent maximum theoretically possible maltose)

Per cent starch	Hours of incubation			
	12	24	36	48
0.5	22.7	47.9	51.7	51.7
1.0	24.7	52.4	54.1	46.7
2.0	18.4	41.8	44.2	48.9
3.0	11.4	39.2	41.4	41.4
5.0	8.5	38.6	38.1	47.2
10.0	3.8	18.5	22.8	26.3

Saccharification was apparently completed after one day of incubation, because the increase in reducing substances between 24 and 48 hr. of incubation was comparatively small when compared to that obtained during the first 24 hr. Results after 24 hr. were probably no longer indicative of starch saccharification by amylase.

One per cent soluble starch seemed to be the optimum concentration for saccharification under the conditions of this experiment. Ten per cent of soluble starch was saccharified by *B. stearothermophilus.*

Discussion

The inability of certain commonly used, commercial protein media to support the formation of amylase by *B. stearothermophilus* cultures was a significant observation.* Good growth of the bacteria in a starch-containing medium is apparently not enough to ensure the hydrolysis of starch. The implications for taxonomic studies are at once obvious. Crowley (4) described the role of amino acids for the activity of amylase and of other enzymes of hemolytic streptococci. Hokin (6) reported on the effect of certain amino acids on amylase synthesis by pigeon pancreas slices *in vitro.* It is possible that the amino acid composition of the medium, both qualitatively and quantitatively, determines whether or not amylase will be formed by bacteria. Studies along these lines are in progress in our laboratories.

B. stearothermophilus hydrolyzed starches under a wide variety of cultural conditions. Five different starches coming from different manufacturers and distributors were hydrolyzed within four days of incubation at 65° C. Quantitative differences, judged by the ease of the initial attack and by the extent of subsequent hydrolysis, existed between batches of the same starch sometimes to a larger degree than between different brands. However, as long as the starch concentration was kept sufficiently low, all cultures hydrolyzed starch. Although some cultures were unable to attack 1% starch under the conditions of the experiment, others hydrolyzed 10% soluble starch readily. Length of the incubation period was another important factor. The cultures grew within a few hours at 65° C.; yet, several days were sometimes required for the hydrolysis of starch. Neither the initial pH nor the subsequent pH changes of the medium influenced the breakdown of starch. The cultures hydrolyzed the starch regardless of acid or alkaline reactions. Certain cultures never formed any acid from starch. For this reason, acid formation is an unreliable criterion for the hydrolysis of starch. Likewise, certain cultures never formed any reducing sugars from starch. It was possible that the sugars were formed, but used up again by the time the test was performed. In either case, the formation of reducing sugars from starch constitutes an unreliable criterion for hydrolysis. The fate of the starch must be known. This is best ascertained by the conventional iodine color test.

False positive iodine tests, indicating the hydrolysis of starch when none has occurred, may be caused by the physical arrangement of the starch molecule, by complexing of the starch with unsaturated substances (e.g. fatty acids) and by reactions of the starch with aldehydes and alkalies (9). Negative tests,

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* *The writers have observed recently that the same was true for 24 Salmonella cultures comprising 16 species. The preventive effect of certain protein media on amylase formation is therefore not limited to spore-forming bacteria only.*

yielding a blue color with iodine, are probably most often caused by unfavorable cultural conditions: amylolytic cultures did not hydrolyze the starch under the conditions of the experiment. This has led to numerous contradictory reports in the literature concerning the starch-hydrolyzing ability of species. Inadequate cultural conditions contribute very little to a better understanding of a bacterial species. It is the duty of the investigator to provide favorable conditions, even when they are not "standard conditions".

In this connection, the results obtained in starch broth and on starch agar media are of interest. More cultures attacked starch in the broth than in the same medium with agar added. The factors contributing to the formation of a zone of hydrolysis in a solid medium are very little understood at present. Therefore, for taxonomic work broth cultures are to be preferred over agar cultures.

B. stearothermophilus hydrolyzed starch readily at 65° C. when incubated sufficiently long in liquid media containing favorable proteins and starch in low concentration.

Acknowledgments

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References

1. Blom, J., Bak, A., and Braae, B. Alpha Amylasen—Beta Amylasen. Z. physiol. Chem., 250 : 104–122. 1937.
2. Breed, R. S., Murray, E. G. D., and Hitchens, A. P. Bergey's manual of determinative bacteriology. 6th ed. The Williams & Wilkins Co., Baltimore. 1948.
3. Coolhaas, C. Zur Kenntniss der Dissimilation fettsaurer Salze und Kohlehydrate durch thermophile Bakterien. II. Die Dissimilation von Staerke und Zuckerarten durch thermophile Bakterien. Zentr. Bakt. Parasitenk. Abt. II. 75 : 344–360. 1928.
4. Crowley, N. The effect of amino-acids and other substances on the activity of streptococcal hyaluronidase. J. Gen. Microbiol. 5 : 906–918. 1951.
5. Gaughran, E. R. L. The thermophilic microorganisms. Bact. Revs. 11 : 189–225. 1947.
6. Hokin, L. E. Amino-acid requirements of amylase synthesis by pigeon pancrease slices. Biochem. J. 48 : XI. 1951.
7. Imsenecki, A. A. and Solntzewa, L. I. The production of amylase preparations from the culture of thermophilic bacteria. Microbiologiia, S.S.S.R. 13 : 54–64. 1944. (In Russian.)
8. Imsenecki, A. A., Solntzewa, L. I. and Kuzyurina, L. A. Thermophilic amylolytic bacteria. Mikrobiologiia, S.S.S.R. 11 : 29-45. 1942. (In Russian.)
9. Kerr, R. W. The chemistry and industry of starch. 2nd ed. Academic Press Inc., New York. 1950.
10. Proskuryakov, N. I. and Dimitrievskaya, N. V. Some properties and the active groups of specimens of alpha-amylase of thermophilic anaerobes. Compt. rend. acad. sci. U.R.S.S. 67 : 699–702. 1949.
11. Stark, E. Stenothermophilic bacteria and their starch-splitting enyzmes. Ph.D. thesis. Purdue University. 1951.
12. Stark, E. and Tetrault, P. A. Observations on amylolytic bacteria. I. A survey of named mesophilic species on soluble starch. Can. J. Botany, 29 : 91-103. 1951.
13. Stark, E. and Tetrault, P. A. A determinative study of amylolytic stenothermophilic bacteria isolated from soil. Sci. Agr. 32 : 81–92. 1952.
14. Underkofler, L. A., Guymon, J. F., Rayman, M. M., and Fulmer, E. I. A semimicromethod for the determination of the reducing sugars in fermentation media. Iowa State Coll. J. Sci. 17 : 251–256. 1943.

FREQUENCY OF MICRONUCLEI IN POLLEN QUARTETS OF COMMON WHEAT MONOSOMICS[1]

By J. W. Morrison[2] and John Unrau[3]

Abstract

The frequency with which 20 different monosomes of the common wheat variety, Chinese Spring, formed micronuclei in pollen quartets was determined. It was found that unless the study was made at an early developmental stage characterized by a distinct cell wall surrounding the quartets, the counts were unreliable, because some micronuclei were lost. The frequency of micronucleus formation was similar for anthers of a floret, florets of a spike, and plants of a monosome. Among the monosomes studied, there were three groups of three and four of two in which the total frequency of quartets with micronuclei, and the distribution of numbers of micronuclei per quartet, were strikingly similar. In the case of the groups of three, two monosomes were from the *A* and *B* genomes while one was from the *D* genome. This is interpreted as evidence of homoeology of chromosomes of a group and also that such chromosomes have undergone less change than those that do not form such series.

Introduction

Nullisomics and monosomics are rapidly becoming more and more important in breeding and genetic projects involving common wheat. In genetic analyses certain characteristics can be associated with specific chromosomes, while in breeding whole chromosome substitutions offer a new and surer method of transferring desired characteristics. More and more geneticists and plant breeders are getting projects under way involving nullisomics or monosomics.

Since, in the case of most monosomes, it is impossible to recognize the monosomic condition phenotypically, it is necessary to make cytological examinations of the breeding material. The monosomic condition can usually be easily and quickly determined at microsporogenesis. At metaphase I the 20 bivalents are normally found at the plate while the univalent is off the plate. At anaphase *I* the univalent usually splits equationally at the equatorial plate and one or both halves frequently fail to be incorporated in the telophase I nuclei. At ana- and telophases II the split halves, because of lagging, again frequently fail to reach the quartet nuclei, in which case they form micronuclei. Since presence of micronuclei in quartets is commonly used in identifying monosomics, it is important that the frequency with which each of the 21 monosomes form micronuclei under standard conditions be determined.

A study of the frequency with which the different monosomes from micronuclei in pollen quartets (tetrads) should give information on a number of

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additional questions. If the chromosomes of each of the three different genomes are distinct, and if within a genome there is a similar behavior pattern, one might expect a similar frequency for three sets of seven. In fact, work by Sax (5) would support such a condition, for in a study of meiosis in a triploid hybrid he found no first division splitting and consequently no second anaphase lagging of the *B*-genome univalents. One would expect, therefore, one group of seven of the tetraploid (the *A* and *B* genomes) in which there would be very few quartets with micronuclei.

On the other hand, if there are series of homoeologous chromosomes in the different genomes, this might possibly be indicated by similar behavior in micronucleus formation, i.e., there would be series representing three chromosomes with similar frequency of micronucleus formation. Sears (6) has demonstrated tbe existence of such series since certain tetrasomics compensate for the loss of certain pairs of chromosomes. Finally, such a study would reveal the relative stability of different monosomes. Sears (7) and Sanchez-Monge and MacKey (4) have found that misdivision is fairly frequent with at least one monosome. There is some danger that wheat breeders and geneticists regard monosomes as entirely stable.

Materials and Methods

Twenty different monosomic lines of Chinese Spring wheat were used in this study.[1] Uncontrolled pollination of monosomics results in nullisomic, monosomic, and normal progeny. Monosomic plants for study of pollen quartets were selected by cytological examination of metaphase I.

Entire spikes of selected plants were killed and fixed in Carnoy's fluid A. Cytological examinations and photomicrographs were made from fresh aceto-carmine smear preparations.

Preliminary observations showed that magnification and stage of quartet development might affect the frequencies of quartets with micronuclei. A study was therefore undertaken to determine the critical stage of development for all subsequent determinations. The magnification found to be satisfactory was 240×. Further it was found that only slight pressure could be used in preparing the slides, consequently focusing had to be done at various levels.

To determine whether frequency of micronucleus formation was constant for a given monosome, different plants, florets, and anthers were studied.

A final examination of all monosomics was made with quartets at the critical stage and using the technique found most satisfactory in previous determinations. In this final study quartets were scored as (*a*) with, and (*b*) without, micronuclei; but in those with micronuclei the number per quartet was noted. Three different plants were used for each monosome and the examination was made on approximately 500 quartets per plant.

[1] *Included in the study was an additional line obtained by Dr. H. Kihara from a T. spelta × T. polonicum derivative which was thought at the time to complete the series, but which has since been found to be XXI. Monosomic XIV was not available when this study was begun.*

Experimental Results

Frequency of Micronuclei in Young and Old Quartets

The results of this study made on one plant of monosome III and one of monosome II are summarized in Table I. As can be seen, older quartets in every case had a much lower frequency with micronuclei. There were two main causes for this lower frequency in older quartets. Firstly, micronuclei frequently formed microcytes and even the slightest pressure forced them out of the quartet arrangement. (Progressive stages of this are shown in Fig. 1, E, F, and G.) Secondly, in older quartets micronuclei were often observed to be diffuse and indistinct. Whether such micronuclei were actually absorbed into the cytoplasm was not determined, although this has been suggested by Thompson (8) and more recently by Frankel (2).

It is significant to note that the counts on the plant from monosome II were made after the stage was designated as young reliable or old and questionable. In all three cases when young quartets were classified the frequency was very similar and also much higher than in the older quartets.

These results show definitely that reliable and comparable counts can be made only when no loss of micronuclei has occurred, since the loss might conceivably not be similar for all determinations. The stage determined as reliable was when a distinct wall still surrounded the entire quartet. Quartets at this stage are illustrated in Fig. 1, A, B, C, and D.

TABLE I

FREQUENCY OF MICRONUCLEI IN OLD AND YOUNG QUARTETS

Monosome studied	Plant No.	Count No.	No. of Qs. counted	Qs. with Mn. in %	Stage of Qs. development
III	98A–2	1	517	32.9	Old
		2	588	48.6	Young
		3	554	56.5	Young
		4	389	37.0	Old
		5	619	50.9	Young
II	97A–21	1	641	66.3	Young, reliable
		2	555	47.8	Old, questionable
		3	753	65.6	Young, reliable
		4	710	67.5	Young, reliable

Frequency of Micronucleus Formation Within Monosomic Plants

The results from a study of different anthers within a floret are presented in Table II. As can be seen from the results all anthers from a floret had similar frequencies of quartets with micronuclei. Similarly, the data in Table III show that the frequency of micronucleus formation was consistent for different florets of a plant and also for different plants of a monosome.

TABLE II

FREQUENCY OF MICRONUCLEI IN QUARTETS OF DIFFERENT ANTHERS OF A FLORET

Monosome studied	Plant No.	Anther No.	No. of Qs. counted	Qs. with Mn. in %
XII	07–2	1	242	39.7
		2	245	41.2
		3	222	42.8
IV	99–5	1	186	66.7
		2	243	65.0
		3	214	65.9
XX	15A–9	1	303	54.5
		2	367	54.2
		3	247	55.5
XXIa	13–19	1	360	51.7
		2	318	48.7
		3	214	52.8

TABLE III

FREQUENCY OF MICRONUCLEI IN QUARTETS FROM DIFFERENT FLORETS OF A PLANT

Monosome studied	Plant No.	No. of Qs. counted	Qs. with Mn. in %
V	00–22	738	56.8
	"	636	56.9
X	05–4	560	36.3
	"	620	34.8
XI	06–5	621	50.7
	"	625	50.2
XIV	09–18	837	58.3
	"	597	57.1
	09–25	540	55.6
	"	607	51.1
XVI	11A–20	601	55.9
	"	670	57.6
XXI	16–16	631	46.9
	"	554	46.4
XXI*a*	13–19	804	50.0
	"	892	50.9

Reliable counts for a monosome can, therefore, be obtained from any plant or floret, provided the quartets are at the critical stage of development.

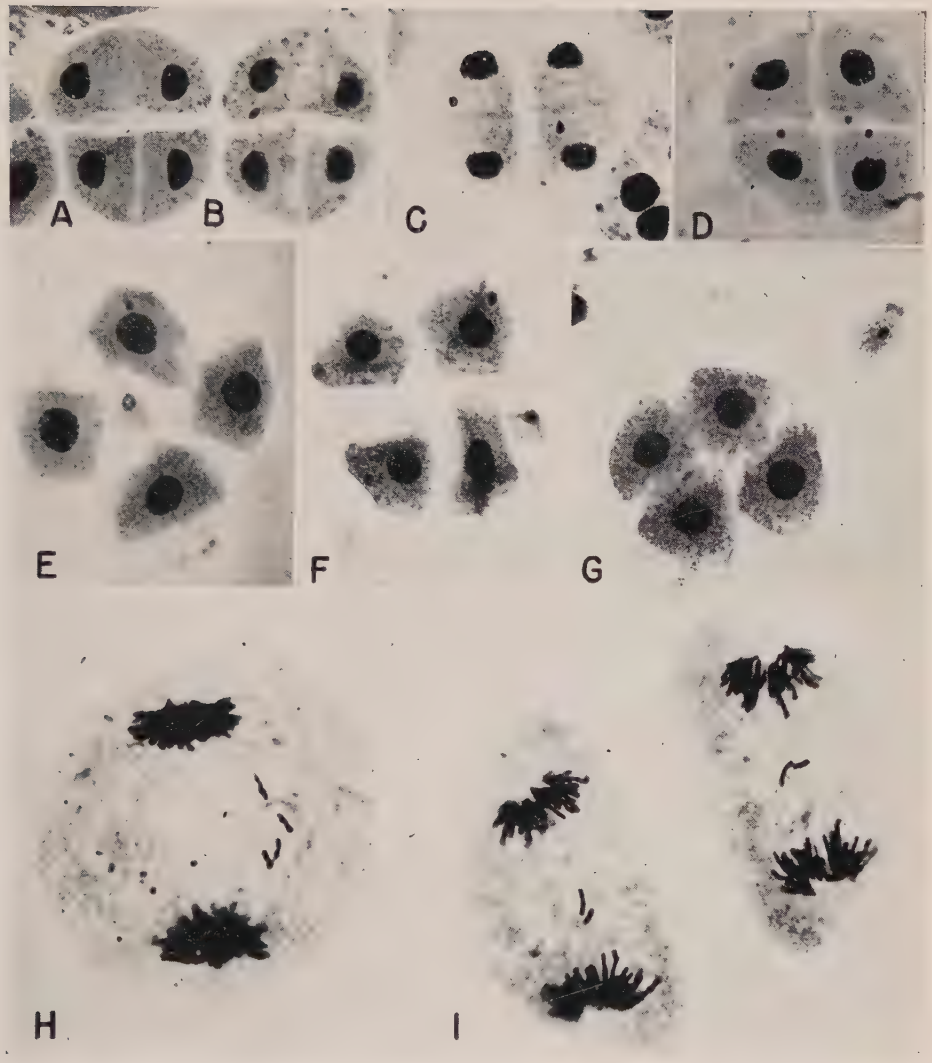

FIG. 1. Micronuclei in pollen quartets and misdivision of univalent chromosomes.

A, B, C, D: Quartets at critical stage of development with 0, 1, 2, and 3 micronuclei per quartet respectively. The distinct surrounding cell wall is clearest in D.

E, F, and G: Progressive stages in loss of micronuclei as microcytes from quartets that are too old.

H: Late anaphase I of meiosis showing misdivision (fragmentation) of one chromatid of the lagging univalent.

I: Anaphase II. Misdivision in the two halves of the univalent chromosomes. It is apparent that misdivision is occurring in the same region in both chromatids. (Magnification approximately 800×.)

Determination of Micronucleus Frequency in Quartets of All Monosomes

The results of this determination made on three plants for each monosome and on at least 500 quartets per plant are summarized in Table IV.

TABLE IV

FREQUENCY OF QUARTETS WITH MICRONUCLEI IN 20 MONOSOMIC LINES OF COMMON WHEAT

(Final determination)

Monosome studied	Qs. analyzed No.	Per cent frequency with micronuclei	Number per quartet				
			1	2	3	4	Over 4
I	1594	39.0	26.6	10.6	1.4	0.4	0.00
XII	1832	40.4	23.3	14.7	1.9	0.4	0.00
XV	1800	40.6	24.8	13.7	1.3	0.8	0.04
II	1865	65.2	30.9	27.7	5.3	1.0	0.20
XIII	1602	62.9	31.0	25.8	4.5	0.9	0.60
XX	1946	63.3	27.8	29.8	4.6	1.0	0.20
III	1957	47.8	26.7	17.0	3.5	0.6	0.00
IX	1641	47.7	24.9	16.2	4.9	1.3	0.50
V	2108	55.5	27.2	22.0	4.5	1.3	0.30
XVIII	1777	55.1	27.2	24.3	4.0	0.8	0.60
VI	1792	49.7	32.4	15.4	1.7	0.1	0.00
XVII	1695	50.1	31.7	14.4	3.2	0.6	0.20
VII	1774	46.5	25.9	16.5	3.5	0.5	0.10
XI	1879	47.4	25.8	18.5	2.6	0.5	0.00
XXI	1819	44.9	25.9	16.4	2.4	0.2	0.00
VIII	1651	34.3	19.4	11.3	2.9	0.4	0.10
X	1946	34.1	19.8	11.0	2.2	0.1	0.00
IV	1795	64.8	29.0	28.2	5.6	1.5	0.50
XVI	1698	57.4	32.2	21.8	3.2	0.3	0.00
XIX	2011	60.2	35.5	19.3	4.4	0.5	0.40
XIXa	2012	50.2	25.2	18.4	4.6	1.6	0.40
L.S.D.		3.8					

When monosomes with similar frequencies are arranged together, the results are significant in several respects. There are three series of three each where the total frequency and the frequencies of one, two, or more micronuclei per quartet are strikingly similar. Moreover, in each of these series there are two chromosomes from the tetraploid genomes *A* and *B*, and one from the *D* genome. From the compensating effects of tetrasomes for nullisomes, Sears (6) has suggested the following homoeologous series: (1) II, XIII, XX; (2) VII, XI, XXI; (3) VI, X, XIX; (4) III, XII, XVI; and more recently[2] V, IX, and

[2] *From a personal communication.*

XVIII. Our data show consistent similar micronucleus formation for the first two and partly for the last series, but very definitely do not show similarity between chromosomes of the other two series. It should be pointed out though that in the case of the Series V, IX, and XVIII, chromosomes V and XVIII are very close but IX is significantly out of line.

The behavior of monosome XXI*a* is of interest. As indicated earlier, this monosomic was obtained from a pentaploid wheat hybrid involving *T. spelta* and *T. polonicum*. While the total frequency is different, distribution of quartets with one and two micronuclei is very similar. This monosome does, however, have a much higher frequency of quartets with three or more micronuclei than does the Chinese Spring monosome XXI. This may be caused by either higher misdivision frequency of the monosome, or less regularity and stability in the meiotic behavior of the other chromosomes of this line.

With respect to the frequency distribution of quartets with one and two micronuclei, it is evident that, in general, where the total frequency was high, the relative proportion of those with two micronuclei also was high. This is illustrated by the results from II, XVIII, XX, and IX. Monosome XIX definitely is an exception, having high total frequency but a lower proportionate frequency of quartets with two micronuclei. It is also evident that when the total frequency was low, the proportion of quartets with two micronuclei was low. Thus in the Series I, XII, XV, VIII, and X, the proportion of quartets with two is almost half that with one as contrasted to the Series II, XIII, XX, where these two classes are almost equal. This was to be expected if frequency of micronucleus formation is associated directly with lagging of univalents. When the extent of lagging is greater, one would expect a greater proportion of cases where both halves of the split univalent were excluded from the telophase II nuclei.

Quartets with more than two micronuclei might possibly have two main sources. Firstly, they might result from chromosomes other than the monosome. Secondly, fragmentation of the monosome could result in quartets with more than two micronuclei. Such fragmentation can occur at both meiotic divisions and is illustrated in Fig. 1, H and I.

As in the case of total frequency and the distribution of one and two micronuclei per quartet, the frequency of quartets with three or more is different for different monosomes. Again, however, the pattern within a series is very similar. Higher frequencies are generally present in those monosomes that have higher total frequencies, although this relationship was not completely consistent.

These different values for quartets with three or more micronuclei may be caused by differences in stability i.e. misdivision of the univalent, differences in lagging of fragmented univalents, differing effects of a certain monosome on the stability of the other chromosomes, or a combination of these factors. It is also possible that if lower frequency of micronuclei in quartets is caused by fewer monosomes splitting at the first division there also would be fewer lagging second anaphase chromosomes which could misdivide, thus resulting in fewer quartets with the higher numbers of micronuclei.

Discussion

From the results of the preliminary and second determinations, and also from the determination of the critical stage, it is evident that quartets should all be examined when they are still within the pollen mother cell envelope. When this is done, the frequency for any monosome is consistent for different plants, different florets, and different anthers. This is evidence that the frequency with which different monosomes from micronuclei is causally related to factors or forces inherent in the chromosome itself. Differences in frequency therefore, represent differences in these inherent factors in individual chromosomes.

The results of our determination definitely indicate similarities and differences in frequency of micronucleus formation among the 20 different monosomes studies. The data therefore do not support the results of Sax (5) that chromosomes of the *B* genome all behaved similarly and did not split at Division I. If these chromosomes never split at the first division there should have been seven monosomes in the group from I to XIV which rarely or never formed micronuclei. Rather, these results support the findings of Aase (1) who reported that whether or not splitting occurred at the first division depended on the position of the univalent on the spindle at the time of anaphase I. That is, lagging and consequent micronucleus formation would occur only when the chromosome had split, and since micronuclei were not formed in all quartets, it is evident that splitting did not always occur. There is no justification to assume, however, that the frequency of first division splitting of univalents was directly reflected by the frequency of micronucleus formation, since in some cases the lagging univalents would probably be included in the telophase II nuclei. Obviously, a detailed examination of all monosomes should be made at anaphase I to determine the frequency with which splitting occurs at the first division. Then frequency of micronucleus formation could be related directly to frequency of first division splitting and inferentially to second anaphase lagging.

It is considered highly significant that there are series of chromosomes where total frequency and distribution of one, two, three, or more micronuclei per quartet are similar. This is interpreted as being evidence in support of the McFadden–Sears hypothesis on the origin of common wheat (3). According to this hypothesis, the three genomes had a common origin and it therefore would be quite probable that there still is a great deal of basic similarity or homoeology among chromosomes of the three genomes.

In the course of evolution changes may have been more pronounced in some chromosomes than in others, so that the series would not be expected to be complete in all cases. In any event, the authors feel that when the frequency of quartets with micronuclei and the distribution is similar, it is a definite reflection of similarity of forces or factors inherent in the chromosomes. These forces are likely those primarily concerned with chromosome orientation and movement.

Quartets with three or more micronuclei involve aberrations other than those associated with the ordinary univalent mechanism. The majority of these extra micronuclei are probably the result of univalent fragmentation or misdivision. Sanchez-Monge and Mackey (4), who studied misdivision in chromosome IX, found a much greater frequency than is suggested by our percentage of quartets with three or more micronuclei. It must be pointed out, however, that the sum of the classes with three or more micronuclei is not necessarily an exact measure of misdivision frequency since some fragmented chromosomes might lag more than others. On the other hand, it is striking that those monosomes with the highest total frequency of micronuclei also have the higher frequencies of quartets with three or more micronuclei. If these chromosomes lag more there would be greater opportunity for misdivision. Similarly, if lagging initially results from first division splitting, there would be more split univalents that could misdivide.

Obviously, there are several further studies that should be undertaken in order to complete the picture of the univalent mechanism at meiosis. Anaphase I should be studied to determine quantitatively the frequency of first division splitting and of misdivision of the various monosomes. Anaphase II and telophase II should be studied to determine the frequency of misdivisions in these stages for all the chromosomes. These studies have already been undertaken and the results will be reported when they are complete.

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References

1. Aase, H. C. Cytology of hybrids. Wash. State Coll. Research Studies, 2 : 3–60. 1930.
2. Frankel, O. H. A self-propagating structural change in *Triticum*. Heredity, 3 : 163–194. 1949.
3. McFadden, E. S. and Sears, E. R. The genome approach in radical wheat breeding. J. Am. Soc. Agron. 39 : 1011–1026. 1947.
4. Sanchez-Monge, E. and Mackey, J. On the origin of subcompactoids in *Triticum vulgare*. Hereditas, 34 : 321–337. 1948.
5. Sax, K. Sterility in wheat hybrids. II. Chromosome behaviour in partially sterile hybrids. Genetics, 7 : 513–552. 1922.
6. Sears, E. R. The use of nullisomics in wheat breeding. Proc. 5th Meeting Assoc. Comm. Plant Breeding. Sub. App. "a" pp. 1–3. 1950.
7. Sears, E. R. Personal communication to the junior author.
8. Thompson, W. P. Chromosome behaviour in triploid wheat hybrids. J. Genetics, 17 : 43–48. 1927.

MICROCALORIMETRIC STUDIES ON GERMINATIONS OF CEREALS[1]

By H. Prat[2]

Abstract

Experiments have been performed on seedlings of many species of cultivated plants with a new Tian-Calvet microcalorimeter installed at the University of Montreal. The characteristic elements of the curve of thermogenesis are first described on wheat germinations and their variations discussed in function of temperature, preliminary dehydration, substances in solution in the soaking liquid: salts, alcohol, auxins, etc. Then comparisons are made between germinative thermogeneses of oats, rye, barley, corn, flax, tomatoes, etc., showing the numerous possible applications of microcalorimetry in plant studies and agronomy.

I. Apparatus

Thanks to a grant of the National Research Council we have installed in the Institute of Biology, University of Montreal, a new type of microcalorimeter Tian-Calvet (2) fitted with the last improvements: four calorimetric blocks grouped by pairs in opposition on two high-sensitivity galvanometers, the whole installation being included in an insulated envelope with thermoregulation. By comparison with the primitive apparatus of Tian (14, 15) the following advantages are gained:

(*a*) Grouping the calorimeters by pairs in opposition makes possible a selective recording of the thermic effects of a single phenomenon, eliminating from the record any heat productions occurring symmetrically in the two opposed blocks.

(*b*) Including the galvanometers in the same insulated envelope as the calorimeters themselves eliminates the trouble of odd thermoelectric effects in the connecting circuits.

(*c*) The envelopes being entirely made of copper, aluminum, and asbestos, the water-mass of the ancient apparatus is suppressed, eliminating its numerous inconveniences (humidity damaging the apparatus in spite of dehydrating buffers, etc.).

(*d*) Thermoregulation of the envelope gives the possibility of operating at any given temperature between 15° and 40° C. Eventually this range will be expanded to 0°, by adjunction of refrigerating devices.

(*e*) The use of four calorimetric blocks, two galvanometers, and two recording drums allows the simultaneous performance of two entirely different series of experiments, provided that the same temperature may fit both.

(*f*) Each apparatus can work on three sensitivities, the highest (GS) being obtained by using 128 thermoelectric couples surrounding the calorimetric chamber, the medium (MS) with 16 couples, and the smallest one (PS) with

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the same 16 couples plus an additional resistance. The ratio of the three sensitivities is about as 1, 2.9, and 14. With the highest sensitivity it is possible to record heat productions as small as 0.00001 cal.

II. Thermogenesis of Wheat Germination

As soon as water is put in contact with dry seeds we observe first a quick production of heat (Fig. 1, *OA*), then a depression (*BC*), then a new and more slowly growing thermogenesis (*CD*). We have described these stages in many previous publications (4, 5, 8, 9, 11) and called the first part of the curve (*OAB*) "*physico-chemical thermogenesis*"; it represents the summation of various physical and chemical processes taking place in the soaking of the dry grain (dynamic part of the hydro-stage): water adsorption, imbibition, and swelling of the colloids, dissolution, etc. Some of them are exothermic, others endothermic. At the beginning the rise of thermogenesis is very sharp (*OA*), reaching a peak in less than half an hour. During this period the processes of water adsorption on the dry matter of the seed are probably dominant and account for the greatest part of the heat produced. Then, after the peak *A*, the curve begins to decrease, more and more slowly. In the example of Fig. 1 (wheat grains at 24° C.), thermogenesis fades away about four hours after the soaking of the seeds. Then occurs a latent phasis or "*dead time*", *BC* (temps mort). In some cases it corresponds to an absorption of heat, endothermic processes taking then the pre-eminence; in other cases it remains slightly over

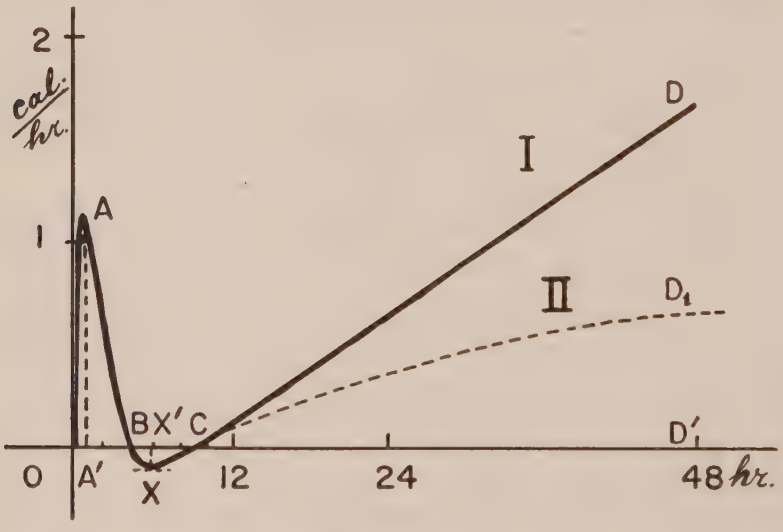

FIG. 1. Thermogenesis of wheat germination. Temperature: 24° C.; darkness; weight of the dry seeds: 1 gm.; soaking with pure water. Curve I (solid line): normal development of seedlings, the amount of soaking water being only 1 cc. Curve II (dotted): seedling placed under conditions of partial asphyxy; the grains are drowned in an excess of water (2 cc.). On abscissae the time, in hours; on ordinates, the thermic flux, in cal. per hour. *OAB*: physico-chemical thermogenesis; *BC*: time of latence; *CD* and CD_1: biological thermogenesis. *X*: minimum of thermogenesis. Portion *BXC* of the curve is endothermic.

zero or may be exactly void; but always this dead time is present as a neat depression of the curve. As to the shape of this latter, the dead time may appear as a horizontal section between points B and C, or as an incurved one, with a marked minimum X. In the example of Fig. 1 the position of this minimum is given by $OX' = 6$ hr.

After point X, the curve again rises and we enter at point C in the third phasis, which we named "*biological thermogenesis*" (4) (beginning of the thermo-stage). From this moment onward the heat is really produced by the metabolism of living tissues, the respiratory rate increasing steadily. In our example, 48 hr. after soaking the heat production reaches almost two calories per hour for 1 gm. of seeds (at 24° C.).

That the first part OAB of the thermogenesis is due only to physico-chemical phenomena is demonstrated by the following fact: when the experiment is performed with grains previously killed through heating at 100° C., this first part OAB remains unchanged. Conversely the biological nature of portion CD of the curve is proved by two other facts: (*a*) when the grains are killed this part of the thermogenesis does not occur; (*b*) on living seeds it is modified by the respiratory conditions: On Fig. 1 we have represented by a dotted line CD_1 (Curve II) the thermogenesis occurring when an excess of water is used for soaking. In this case the grains are drowned and the thermogenesis is lowered: fermentations produced under such conditions of asphyxia give a smaller production of energy than the normal processes of respiration observed when the seedling is well supplied with oxygen.

We have compared the thermogenesis of many varieties of wheat, namely: Blackhawk winter wheat, Henry spring wheat, Saunders wheat (see Table IV). The maximum of physico-chemical thermogenesis is about the same for the three at a given temperature and at comparable states of ripening and preservation. But the duration OB of this first phasis is a little shorter and the beginning C of the biological thermogenesis occurs a little earlier with the spring wheats than with the winter varieties.

III. Influence of Temperature on Germinative Thermogenesis

The curve of thermogenesis is modified by the surrounding temperature (12). Fig. 2 gives a comparison of the curves obtained at 17°, 23°, and 29° C. (Winter wheat). It may be noticed that, within those limits, the elements of the curve measured on the time scale are shortened when temperature rises; conversely the ordinates (thermic flux) are exaggerated. In other words all the processes are hastened and their intensity increased when the temperature is higher. It may be noticed that the total amount of heat produced during the first phase (physico-chemical thermogenesis) remains about constant; it is only given in a shorter time. Also, when temperature is increased, the second phasis (dead time) becomes more obviously endothermic; the third phasis (biological thermogenesis) begins sooner and produces a greater amount of heat. Naturally those conclusions are valid only if the experiments are practised below the optimum temperature, a condition realized in the case of Fig. 2.

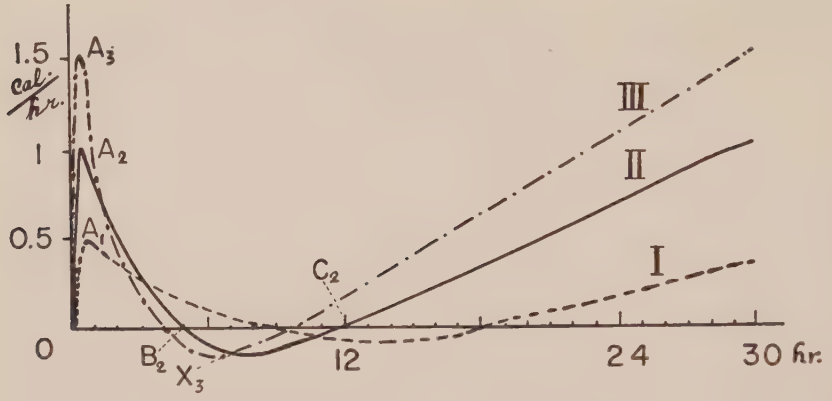

FIG. 2. Germinative thermogenesis of wheat at three temperatures: Curve I (dotted) at 17° C.; Curve II (solid line) at 23° C.; Curve III (dash and dots) at 29° C.

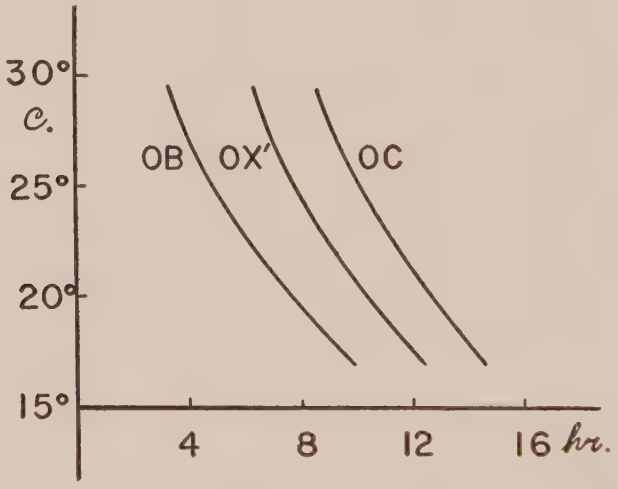

FIG. 3. Variation of the primary characteristics *OB*, *OX'*, and *OC* of the thermogenetic curve of wheat according to the surrounding temperature. On ordinates, the temperatures in degrees centigrade; on abscissae, the times, in hours.

Fig. 3 gives directly the variations of elements *OB*,*OX'*, and *OC* in function of temperature. It emphasizes the necessity to operate always at a same temperature when different lots of seeds are to be compared. If this condition is satisfied the values *OB*, *OX'*, and *OC* may be used as primary characteristics of the thermogenetic curves, in order to compare different species.

IV. Influence of Preliminary Dehydration on Germinative Thermogenesis

If seeds are previously submitted to dehydration, their germinative thermogenesis is strongly increased when, afterwards, they are soaked (7, 10). Fig. 4 represents the thermogenetic curves of wheat grains previously vacuum-desiccated in the presence of phosphoric anhydride during two days (Curve II)

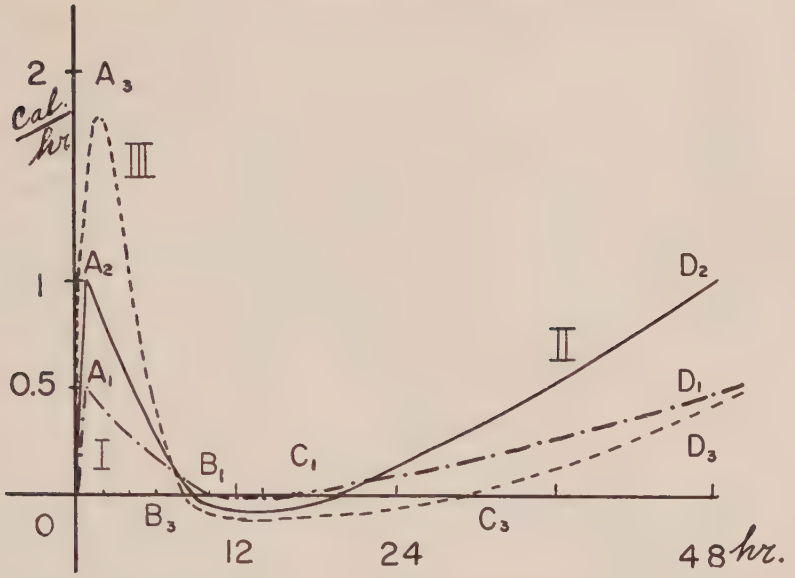

FIG. 4. Thermogenesis of wheat grains previously dehydrated during two days (Curve II, solid line) and 24 days (Curve III, dotted). Curve I (dash and dots) figures the control.

and 24 days (Curve III). Curve I gives the control: seeds recently harvested, taken without any special dehydration. It may be noticed that in Curve III the physico-chemical thermogenesis reaches a peak A_3 four times greater than in normal conditions and in Curve II, two times. The total amount of heat produced during this phase is increased in proportion, the duration *OB* being only weakly modified. Through a very strong dehydration we have obtained maxima AA' as much as 12 times greater than in the control (7, 10).

Fig. 5 gives the variations of the maximum AA' and also of the times *OB* and *OC* at 17° C. in function of the loss of water of the grains, loss expressed in per cent of the initial weight. This figure shows that dehydration shortens but feebly the duration *OB* of physico-chemical thermogenesis, but postpones more neatly the beginning of biological thermogenesis. Thus it increases notably the duration of the dead time *BC*; frequently it renders this latter more strongly endothermic. Table I summarizes the results obtained by one of my assistants, Miss J. Brachet (1), in various conditions of dehydration for a same lot of wheat at 17° C.

The influence of a previous dehydration on the physico-chemical thermogenesis was easy to foresee, as this first part of the phenomenon is given by the hydration heat of the dry material. But, for its influence on the time of latence and on the biological thermogenesis, the experiment only could reveal it. The most interesting result of this series of researches was to demonstrate that a previous dehydration, if it is not too severe, can increase also the biological thermogenesis (D_2, Fig. 4).

When wheat grains are moderately dehydrated, enduring a loss of water equal to about 2% of their weight, their biological thermogenesis is increased

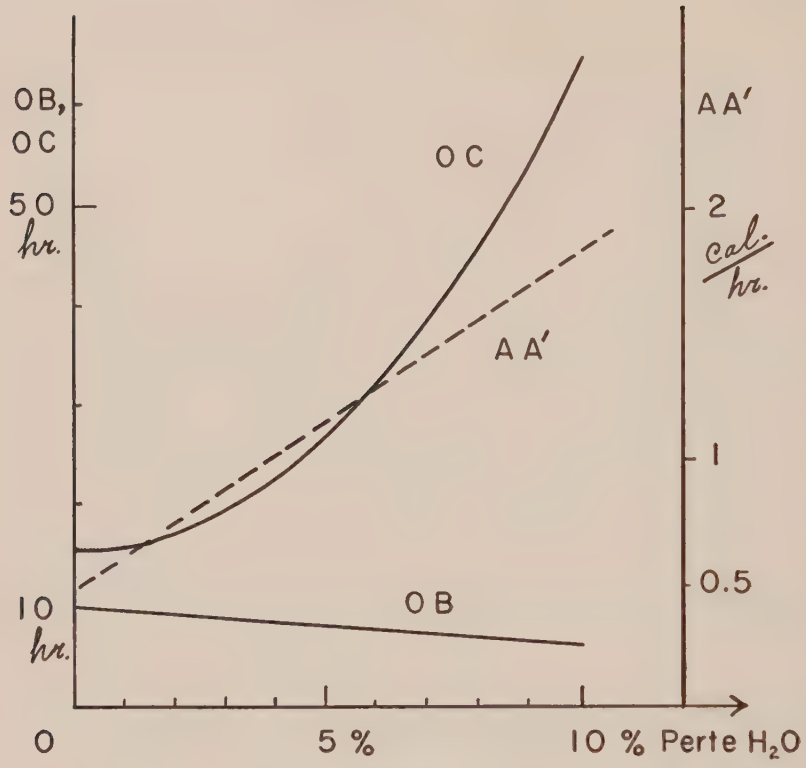

FIG. 5. Variation of the primary characteristics *OB*, *OC* and *AA'* of the wheat thermogenesis according to previous dehydration. On abscissae loss of water expressed in per cent of the initial weight of the seeds. On ordinates, left: the times *OB* and *OC* expressed in hours; right: the values of the maximum *AA'* of physico-chemical thermogenesis, expressed in cal. per hour.

TABLE I

DEHYDRATED WHEAT, 17° C.

Days dehydrat.	Loss of water per gram	Times, hr.			Thermic flux in cal. per hr. per gm.		Heat produced or absorbed, cal. per gm.		
		OB	*OC*	*BC*	*AA'*	*DD'* after 48 hr.	*OAB*	*CDD'*	*BXC*
0	0	10	15	5	0.5	0.5	2.4	6	0
2	0.024	9	20	11	1	1.06	2.9	13.4	−0.3
5	0.044	8	19	12	1.1	0.94	2.6	11.9	−0.7
7	0.058	9	30	21	1.3	0.42	4.4	3.4	−0.9
77	0.100	7	65	58	1.83	−0.1	6.26		−3

and also the growth of the resulting seedling (7). At each moment the length of the first roots, leaves, and internodes may be 10% to 25% greater on the treated seedling than in the control (1).

This observation suggests a practical application: by dehydrating the seeds it could be possible to improve their germinative qualities, as it is done in vernalization. For agricultural practices, facts of hydroperiodism can be as useful to study as facts of thermoperiodism or of photoperiodism.

It must be noticed that if the dehydration is excessive, reaching more than 5% of the initial weight, the germination process can be altered, the dead time *BC* being unduly increased and the biological thermogenesis greatly delayed. This time *BC* may reach as much as three days when the water loss reaches 10%.

V. Influence of Seeds Aging

When a lot of seeds is kept in the laboratory during some months, a slow rise can be observed in its physico-chemical thermogenesis: Experiments performed in October give for instance a value *OA* of 1.2 cal. per gram. But seeds of the same lot examined the next March can give 2 and even 3 cal. per gram (Table IV). This result is not surprising, as the laboratory where the seeds are kept is maintained in very dry conditions all through the winter. Owing to the heating system, the relative humidity remains frequently below 25%. Thus the grains are progressively dehydrated and this fact produces the same rising of the physico-chemical thermogenesis as in the previous experiments. Of course, we may add probably to this physical modification a slow biological process of maturation of the seed, modifying its reactions toward the water intake.

These facts emphasize the necessity to restrain the comparisons to lots of seeds maintained exactly in the same conditions of preservation. The best procedure is to keep all the material in a storage room provided with a constant humidity and a constant temperature, and to take definitive comparisons only after some weeks of storage.

VI. Alternatives of Soaking and Drying

In order to recognize whether these actions are reversible we have submitted wheat seedlings to alternatives of soaking and drying and recorded their thermogenetic responses. Fig. 6 summarizes the results. It appears that the physico-chemical thermogenesis can be indefinitely repeated, but is modified from one test to the following. Its duration is shortened and, conversely, its maximum is increased; thus the total amount of heat produced remains about the same. It seems that a first soaking makes easier the ulterior penetration of water in the seed and that the enzymatic processes producing the biological thermogenesis are more rapidly raised. The latent time becomes weakly exothermic instead of being endothermic or indifferent. Finally the biological thermogenesis is less rapidly growing than after the first soaking.

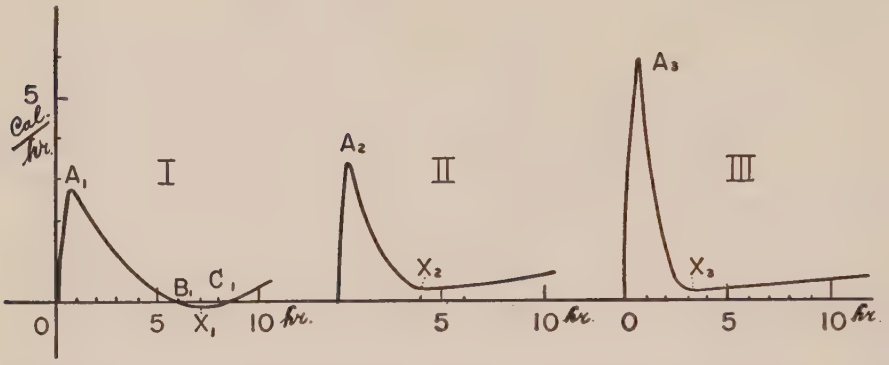

FIG. 6. Influence of alternate soaking and drying on the wheat thermogenesis. From one soaking to the following the physico-chemical thermogenesis becomes shorter and more intense and the endothermic processes disappear.

VII. Influence of Substances Contained in Soaking Water

Investigations have been made also on the influence of various substances on germinative thermogenesis. We have found that a moderate addition of auxin in the soaking water may increase the biological thermogenesis: When indole-3-acetic acid at a concentration of 1 : 10,000,000 (or 0.1 p.p.m., equivalent to 5.7×10^{-7} mole per liter) is put in contact with wheat grains, the physico-chemical thermogenesis is not modified but the biological thermogenesis occurs earlier (6); after 10 hr. instead of 15 hr., at 17° C., and reaches, after 45 hr., a value of 0.4 cal per hr. per gram, almost twice the value obtained with the control in pure water. This observation can be related to the increase of respiratory rates observed through the influence of auxins (3, 13). Robertson Pratt (13) has found a steady increase of the respiration rate of the wheat seedling for concentrations of indole-3-acetic acid reaching up to 100 p.p.m. (5.7×10^{-4} *M*), a rapid depression of respiration being then observed above this limit.

On the contrary, when alcohol is added to the soaking water, the biological thermogenesis immediately is delayed. With 5% of ethylic alcohol, the time of latence is indefinitely prolongated. However the grains are not killed, even not permanently injured, for when they are taken out of the alcoholic solution and put into pure water they germinate normally. This fact may be connected with our previous observations on the lowering of biological thermogenesis due to privation of oxygen (CD_1, Fig. 1), this privation producing an alcoholic fermentation and lowering the rate of thermogenesis. In both above experiments, for the used concentrations of auxin and alcohol, the physico-chemical thermogenesis was not appreciably modified.

Miss J. Brachet has investigated the influence exerted on thermogenesis by the nutrient solution of Sachs and its components (1). With the entire solution the maximum AA' of the physico-chemical thermogenesis is much higher than with pure water: 1.6 cal. per hr. per gram at 17° C. instead of 0.5; conversely

TABLE II

SUBSTANCES IN SOAKING WATER; WHEAT, 17° C.

Medium	Concentrat. gm. per liter	Times, hr.			Thermic flux in cal. per hr., per gm.		Total heat produced or absorbed, cal. per gm.		
		OB	*OC*	*BC*	*AA'*	*DD'* after 48 hr.	*OAB*	*CDD'*	*BXC*
Water	0	10	15	5	0.5	0.5	2.4	6	0
Sachs	2.6	6	14	8	1.6	0.58	3	9	− 0.2
$FeSO_4$	0.1	6	45	39	2.5	0.1	5.32	0.1	−14.6
$CaSO_4$	0.5	6	10	4	0.4	1.02	0.97	16	− 0.2
$MgSO_4$	0.5	5	17	12	0.4	0.42	1.04	4.2	− 0.3
NaCl	0.5	7	15	8	1.06	0.71	2.45	8	0
KNO_3	1	6	12	6	0.37	1.16	1.11	18.5	− 0.1
Knop	2	5	22	17	0.58	0.66	1.20	8	− 0.8

the duration *OB* on this phasis is shortened (6 hr. instead of 10); the dead time BC becomes more neatly endothermic; the biological thermogenesis is but slightly increased (Table II).

When the various components of the Sachs solution are separately investigated (Table II) the following results are observed: iron sulphate at 0.1 gm. per liter gives a strong maximum of physico-chemical thermogenesis (2.5 cal. per hr. instead of 1.6 with Sachs and 0.5 with pure water); the latent phase becomes strongly endothermic and is expanded. This delaying of the biological thermogenesis denotes an intoxication of the seed comparable to the one pointed out by the effect of alcohol. It emphasizes the necessity of a balanced solution, such an intoxication being not present when the entire Sachs solution is used, but occurring only when one of its components, here the iron sulphate, is separately applied.

With calcium sulphate at 0.5 gm. per liter, the physico-chemical thermogenesis reaches about the same maximum as with pure water, but its duration is shortened: 6 hr. instead of 10, meaning a production of heat of about one calorie during the total phase *OAB*, instead of 2.4. The time *OC* is also shortened: 10 hr. instead of 15. The result is that the biological thermogenesis is notably increased, reaching 1.02 cal. per hour and per gram after 48 hr. instead of 0.5, and a total of 16 cal. instead of 6 for the full amount *CDD'*.

Table II summarizes the results obtained with the various salts of Sachs solution. In a whole, all of them tend to shorten the duration of the physico-chemical thermogenesis. Many of them increase the heat production during the two thermogenetic phases: biological as well as physico-chemical. How-

ever a special case remains—that of the sulphate of iron, which strongly increases the physico-chemical production of heat but afterwards considerably delays the biological phasis.

It may be noticed that the concentration of sodium chloride mentioned in Table II: half a gram per liter, represents about 1/60 of that of sea water. However this weak concentration is sufficient to increase notably the thermogenesis of the wheat grains, both in the physico-chemical and in the biological phases.

With the Knop solution the results are comparable to those obtained with the Sachs (see Table II), but the latent time *BC* is more notably increased and the maximum *AA'* less magnified.

VIII. Germinative Thermogenesis of Oats

In the case of oats it is interesting to practise a double series of experiments: one on the seeds included in their paleas, another on the denudated grains. In the second case the peak of the physico-chemical thermogenesis may be increased by about 50%, but the durations of the various phases are not modified.

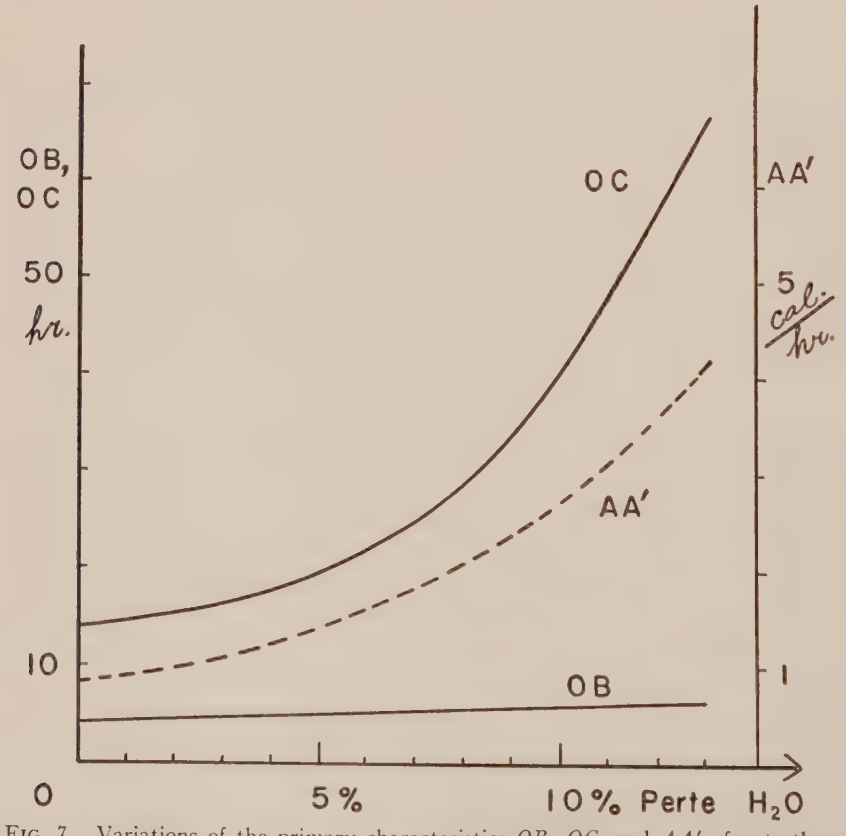

FIG. 7. Variations of the primary characteristics *OB*, *OC*, and *AA'* of oats thermogenesis. Same convention as for Fig. 5.

TABLE III.

DEHYDRATED OATS (17° C.)

Loss of water per gram of seeds	Times, hr.			Thermic flux, in cal. per hr. per gm.		Heat produced or absorbed, cal. per gm.		
	OB	*OC*	*BC*	*AA'*	*DD'* after 48 hr.	*OAB*	*CDD'*	*BC*
0	4	14	10	0.82	0.52	1.22	7.03	−0.6
0.034	4	18	14	0.94	0.61	1.81	7.51	−1.08
0.062	4	30	26	1.76	0.51	3.3	3.78	−3.5
0.11	4	34	30	3.56	0.16	10.8	0.24	−4.2
0.12	6	30	24	4.2	0.54	7.8	4.8	−9.8
0.13	6	66	60	2.86	−0.05	8.1	—	−3.0

Preliminary dehydration modifies the thermogenesis of oats but not exactly as it occurs for wheat. Table III and Fig. 7 summarizes some results obtained with denudated oat grains at 17° C. (1). We can notice that dehydration tends to increase the duration *OB* of physico-chemical thermogenesis instead of to shorten it as for the wheat. But in both cases dehydration increases the maximum of physico-chemical thermogenesis *AA'* and the duration of the latent time *BC*; it postpones the beginning of the biological thermogenesis and increases notably the absorption of heat during the time of latence *BC*. From these results it may be concluded that a preliminary treatment of dehydration is not likely to afford any advantage in the case of oat seeds as it appeared to do in the case of wheat.

IX. Comparisons of Germinative Thermogenesis of Various Cereals and Other Cultivated Plants

Up to now we have observed only small differences of the thermogenetic curves between varieties inside a given species. But strong differences occur from one species to another (Fig. 8). Table IV summarizes the results obtained with 20 varieties of cultivated plants at 24° C. On this table the time *OX'*, moment when the absolute minimum of the curve is reached, is mentioned only when no endothermic phasis exists, whence the impossibility to determine *OB*, *OC*, and *BC*. The single letters: D, J, F, M indicate the month during which the experiments were performed = December, January, February, March. The origin of the seeds is shown by the twin letters between parentheses: (JB): Montreal Botanical Garden; (FE): Central Experimental Farm of Ottawa; (DF): Dupuy and Ferguson.

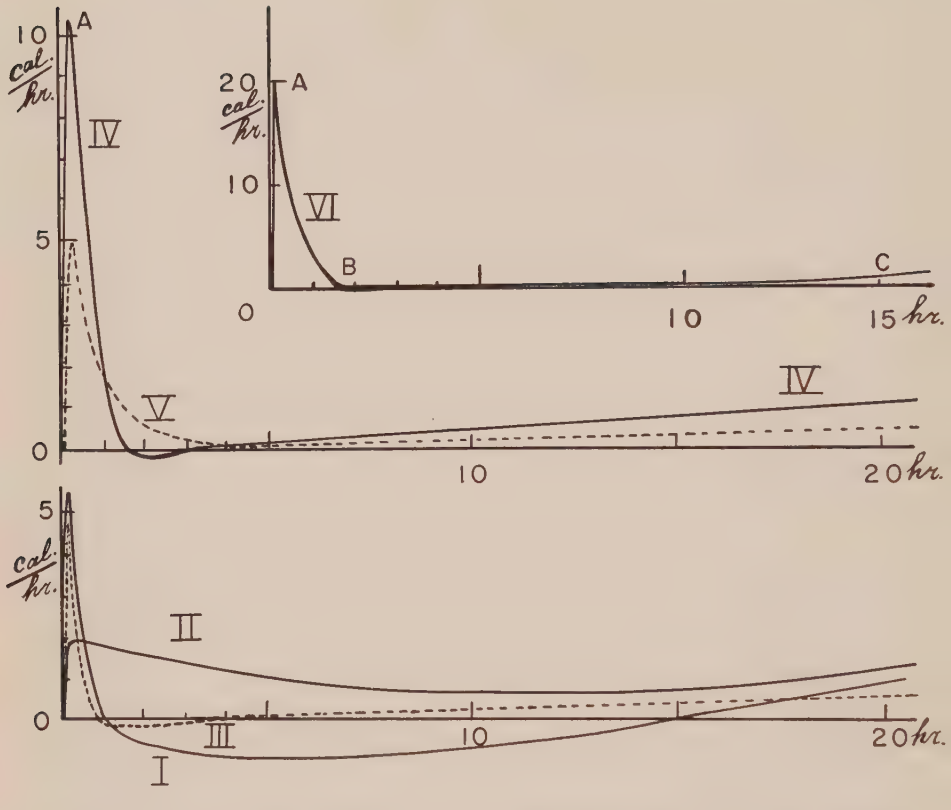

FIG. 8. Germinative thermogenesis of some cultivated seeds: Curve I: celery; II: corn (Golden sunshine); III: cabbage (dotted); IV: tomato; V: beet (dotted); VI: leek. Description of the varieties is given in Table IV. A different scale of ordinates is used for the leek, owing to the exceptionally strong production of heat performed during its physico-chemical thermogenesis.

As a general rule the small seeds display per gram a higher maximum AA' and a shorter time OB for the physico-chemical thermogenesis than the big ones. Those facts are obviously related to the comparatively greater surface offered by the small seeds to contact the soaking water. However the relation is far from being regular, showing that the phenomenon is more complex than a plain physical relation. For instance Table IV shows that carrot seeds possess a higher maximum AA': 8 cal. per hr. than celery seeds (6.4 cal. per hr.); however they are bigger: 880 seeds per gram instead of 2292. Conversely radish seeds offer a greater AA' (14 cal. per hr.) than cabbage and cress (5 cal. per hr), and however are bigger (104 seeds per gram instead of 236 and 552). The biggest seeds examined, corn grains, display a higher AA' than many small grain cereals; but the time OB and OC are longer, processes of hydration of this big mass being necessarily slow.

TABLE IV

THERMOGENETIC CHARACTERISTICS OF SOME CULTIVATED SEEDS (24° C.)

Species	Variety		Number of seeds in 1 gm	Times, hr.				Thermic flux, in cal. per hr. per gm.	
				OB	*OX'*	*OC*	*BC*	*AA'*	*DD'* after 24 hr.
Wheat	Blackhawk, winter	D	32	4		9	5	1	0.5
	" " (JB)	M	32	6		8	3	2.6	0.6
	Henry spring (JB)	D	30	3		6	3	1	0.7
Oats	Beaver, with p. (FE)	D	28	3		5.30	2.30	1.6	0.5
	" "	F	28		6.30			4	1.3
	Beaver, without p.	F	37		6			6	1.9
	Roxton without p. (JB)	F	35	5		9	4	3.5	1.2
Barley	Sanalta (JB)	D	22	4		12	8	0.5	0.5
	"	F	22		7			2.5	1.3
	Oderbrücker (JB)	F	32		8.30			2.5	1.6
Rye	Horton, winter (FE)	J	50		6.30			2	1.2
	Imperial winter (JB)	M	40		7			2	2
Corn	Inbred 103 (FE)	F	4	11		20	9	3	0.6
	N W Dent (JB)	M	4		10			2.1	0.6
	Golden Sunshine (JB)	M	4	7		13	6	2.3	1.1
Cress	No. 1625 (DF)	M	552	1.15		2	0.45	5	2
Cabbage	No. 610 (DF)	M	236	0.45		3.30	2.45	5	0.9
Radish	No. 3608 (DF)	M	104		0.45			14	2
Celery	No. 1143 (DF)	M	2292	1		15	14	6.4	1.9
Carrot	No. 908 (DF)	M	880	0.45		17	16, 15	8	0.3
Beet	No. 765 (DF)	M	56	4		11	7	5	0.5
Leek	No. 2160 (DF)	M	384	1.30		15	13.30	20	0.8
Tomato	No. 4720 (DF)	F	400	1.30		3.15	2	11	1.7
Flax	Rocket CAN 19 (FE)	J	163		4			5	2

As to their taxonomic position, the species and varieties mentioned on Table IV are the following:

I. Graminae: *Triticum sativum* L.: Black hawk winter wheat (JB); Henry spring wheat (JB).

Avena sativa L.: Beaver oats (FE); Roxton oats, semihasting (JB).

Hordeum distichum: Sanalta two rows barley, semihasting (JB), Oderbrucker barley, hasting (JB).

Secale cereale L.: Horton winter rye (FE); Imperial winter rye (JB)

Zea Mays: Inbred corn No. 103 (FE); Northwestern dent corn (JB); Golden Sunshine sugar corn, late (JB).

II. Liliaceae: *Allium porrum.* Elephant leek No. 2160 (DF).
III. Crucifereae: *Nasturtium officinale* R.B. Triple curled cress No. 1625 (DF).
Brassica oleracea L.: Copenhagen Market cabbage No. 610 (DF).
Raphanus sativus L.: "Belle cerise" radish No. 3608 (DF).
IV. Umbellifereae: *Apium graveolens.* White plume celery No. 1143 (DF).
Daucus carota L.: Long perfection Chantenay carrot No. 908 (DF).
V. Chenopodiaceae: *Beta vulgaris*: Detroit dark red beet No. F765 (DF).
VI. Solanaceae: *Solanum lycopersicum*: June pink tomato No. 4270 (DF).
VII. Linaceae: *Linum usitatissimum* L.: Rocket flax C A N 19 (FE).

Conclusions

The newest type of microcalorimeter Tian-Calvet installed last year at the University of Montreal, thanks to a grant from the National Research Council, constitutes an efficient tool in order to investigate the physiological and physico-chemical processes occurring during germination of seeds. The present article is only a preliminary report of results recently obtained with this apparatus, summarized with other data previously obtained with more ancient types of microcalorimeter at the University of Aix-Marseille between 1943 and 1949 (1, 4, 6, 10). At present it is too soon to pretend giving a complete survey of this fairly new field of investigation. However the following points may be mentioned:

1. The general shape of the thermogenetic curve we obtained first on wheat germinations (4) seems to apply, as a general rule, to all the species we have investigated up to now, but with different numerical elements, which may be used as specific characters.

2. Immediately after the contact between water and the dry seed the curve presents: (*a*) a first phasis of rapidly increasing, then more slowly decreasing, thermic flux (*OAB*, Fig. 1), that we named "*physico-chemical thermogenesis*" and which is independent of life, being as well obtained with killed seeds; (*b*) a phasis of depression, often endothermic or weakly exothermic that we named "*dead time*" (*BXC*, Fig. 1); (*c*) a new phasis of increasing thermic flux that we named "*biological thermogenesis*" and which corresponds to the beginning of the growth of the seedling, involving a progressive rising of its respiratory activity (*CD*, Fig. 1).

3. The elements of the thermogenetic curve vary in function of the surrounding temperature. Between 15° C. and 30° C. we have observed that a rise of the temperature shortens the duration *OB* of the physico-chemical thermogenesis and of the time *OC* preceding the start of the biological thermogenesis (Figs. 2 and 3).

4. A preliminary dehydration of the seed increases the value *AA'* of the maximum of thermic flux during the physico-chemical thermogenesis and accentuates the ulterior endothermic processes, when the seed is afterwards soaked (Fig. 4 and Table I).

5. The same preliminary dehydration may provoke also an increase of the biological thermogenesis and an acceleration of the growth, but only under

the condition that it is not too severe. The loss of water must be kept under 5% of the initial weight of the seed; above this percentage, dehydration postpones the appearance of biological thermogenesis (Figs. 5 and 7).

6. The aging of a seed, from the autumn to the spring, provokes a slow modification of the thermogenetic curve, namely an increase of the maximum value AA' of the physico-chemical phasis. This fact seems to be due to a progressive dehydration but also to the maturation process of the seed.

7. Alternatives of moisture and dryness accelerate the physico-chemical thermogenesis, with an increase of its maximum AA' and a shortening of its duration OB (Fig. 6).

8. The thermogenetic curve is modified by substances contained in the soaking water: the biological thermogenesis is increased by indole-3-acetic acid at low concentration, diminished by alcohol and by sulphate of iron. With equilibrated solutions of Sachs and Knop the physico-chemical thermogenesis is emphasized and occurs in a shorter time. Many salts, namely iron sulphate, exaggerate the endothermic processes of the second phasis (Table II).

9. To compare the thermogenetic curves of various plant species the best element to use is the duration of the physico-chemical thermogenesis. This duration may be expressed as OB, if an endothermic phasis occurs, or OX', if there is no endothermy. These times are not strongly affected by the state of dehydration of the seed (Figs. 5 and 7); thus they may be used as primary characteristics of the curve. The time OC, epoch of the beginning of the biological thermogenesis, may be used too, but endures larger variations in function of the state of dryness of the seed.

10. It comes from those observations that, when comparisons between species or varieties are to be done, it is necessary to keep the seeds during several weeks in advance under the same conditions of preservation, and to perform all the experiments at the same temperature.

11. As a general rule the physico-chemical thermogenesis is shorter and reaches a higher maximum per gram with the small seeds than with the big ones. Surface of contact between the seed and the soaking water is obviously involved here. However many other factors intervene: structure of the integuments, nature of the tissues, and of the reserve materials. In such a way no rigorous relation can be established between the size of the seed and its thermogenesis. This latter is truly a specific character and not a mere geometric feature of the grain.

12. From Table IV and Fig. 8 it may be noticed that the investigated Umbellifereae (celery and carrot) are characterized by their strong and short physico-chemical thermogenesis, followed by a strong and long endothermic phasis (Curve I, Fig. 8). The Crucifereae (cress, cabbage, radish) display also a brief and active physico-chemical thermogenesis but, afterwards, the endothermic processes are weak or absent and the biological thermogenesis is precocious and strong (Curve III, Fig. 8). The most powerful production of heat during the physico-chemical thermogenesis is given by tomato (IV, Fig. 8), radish and leek (VI, Fig. 8), which produce as much as 11, 14, and 20

cal. per hour per gram of seed, at their maximum AA'. Concerning the rise of the biological thermogenesis the best results are given by celery, cress, radish, flax, tomato, and some varieties of rye (Table IV and Fig. 8, Curves I and IV).

It results from the above facts that comparison of thermogenetic curves among cultivated plants may be useful to appreciate their specific properties, their reactions to the environment, and the diversified germinative aptitudes of their varieties. In such a way, microcalorimetric investigations are likely to take an interesting place in the field of agronomic research.

Acknowledgments

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References

1. Brachet, J. Influence de la dessiccation et de quelques agents chimiques sur la thermogenèse de la germination. Diplôme d'études supérieures, Faculté des Sciences, Marseille. 1949.
2. Calvet, E. Nouveau micro-calorimètre différentiel et à compensation. Compt. rend. 226 : 1702–1704. 1948. Brevet d'invention No 953.800. France. 1947.
3. Chouard, P. Les progrès récents dans la connaissance et l'emploi des substances de croissance. Rev. intern. botan. appl. et agr. trop. 28 : 189–203 *et seq.* 1948; 29 : 138–156 *et seq.* 1949.
4. Prat, H. et Calvet, E. Application de la micro-calorimétrie à l'analyse des stades initiaux de la germination. Compt. rend. soc. biol. 138 : 662–663. 1944.
5. Prat, H. Distinction d'un hydro-stade et examen des modalités d'action des facteurs externes au cours de la germination. Compt. rend. soc. biol. 138 : 664–665. 1944.
6. Prat, H. Variations de la thermogenèse provoquées par l'acide indolacétique et l'alcool au cours des premiers stades de la germination. Compt. rend. soc. biol. 138 : 675–676. 1944.
7. Prat, H. et Calvet, E. Influence de la déshydratation préalable des graines sur la thermogenèse de germination. Compt. rend. 220 : 226–227. 1945.
8. Prat, H. et Calvet, E. Sur les éléments des courbes de thermogenèse utilisables pour caractériser l'état et les propriétés spécifiques des semences. Compt. rend. 220 : 470–472. 1945.
9. Prat, H., Calvet, E. et Fricker, O. Etude micro-calorimétrique du développement des cultures bactériennes et de la germination des graines. Rev. can. biol. 5 : 247–250. 1946.
10. Prat, H. Variations of thermogenesis during the first stages of seed germination. Trans. Roy. Soc. Can., V, 41(3) : 95–97. 1947.
11. Prat, H. Histo-physiological gradients and plant organogenesis. Botan. Rev. 14 : 603–643. 1948; 17 : 693–746. 1951.
12. Prat, H. Influence de la température ambiante sur la thermogenèse des germinations. Rev. can. biol. 10 : 443–454. 1951.
13. Pratt, Robertson. Influence of indole 3 acetic acid on the respiration and growth of intact wheat seedlings. Am. J. Botany, 25 : 389–392. 1938.
14. Tian, A. Microcalorimètre à compensation par effets Peltier et Joule. Compt. rend. 178 : 705–707. 1924.
15. Tian, A. Recherches sur la calorimétrie. Généralisation de la méthode de compensation électrique; microcalorimétrie. J. chim. phys. 30 : 665–708. 1933.

THE CARBOXYLASES OF LEAVES AND THEIR ROLE IN PHOTOSYNTHESIS[1]

By K. A. Clendenning,[2] E. R. Waygood,[3] and P. Weinberger[2]

Abstract

"Malic" enzyme isolated from the cytoplasm of parsley and sugar beet leaves was linked with illuminated spinach chloroplast fragments to effect photosynthesis *in vitro*. The model photosynthesis system containing excess "malic" enzyme was not inhibited by 5×10^{-4} *M* hydrogen cyanide. The "malic" enzyme system was inhibited by cyanide, however, at very low enzyme concentrations. The richest source of "malic" enzyme found in this study was the mature parsley leaf. Expressed on the same basis, the enzymatic capacities of parsley leaf "malic" enzyme and the Hill reaction capacity of isolated spinach chloroplasts are of similar magnitude. Higher "malic" enzyme and oxalacetic carboxylase activities were found in purified extracts of parsley leaves than in the corresponding root extracts. Oxalacetic, oxalsuccinic, α-ketoglutaric, and pyruvic carboxylases were not inhibited by 10^{-3} *M* hydrogen cyanide. The α-ketoglutaric and pyruvic carboxylases were much less abundant in leaves than in other plant organs; formic dehydrogenase was not detected in leaves although it is abundant in seeds. Glutamic carboxylase was found in the cytoplasm of wheat and sugar beet leaves, and with the aid of $C^{14}O_2$ was shown to be only weakly reversible. No evidence was obtained for the presence in leaf extracts of an enzyme, or mixture of enzymes, capable of decarboxylating phosphoglyceric acid *in vitro*.

Introduction

The enzymes which are responsible for heterotrophic carbon dioxide assimilation have been investigated intensively during the past decade (22, 41). From the standpoint of comparative biochemistry, the same enzymes might be expected to catalyze carbon dioxide assimilation in green plants, and a number of discoveries have been made recently which support this idea. Vennesland and coworkers (7, 9, 15, 30–33) have isolated oxalacetic carboxylase, oxalsuccinic carboxylase, and "malic" enzyme from plant tissue, and have investigated their kinetics and demonstrated their reversibility. Vishniac and Ochoa (34, 35), Tolmach (28, 29), and Arnon (2) have linked isolated chloroplasts with "malic" enzyme from both plant and animal sources to effect net assimilation of carbon dioxide by photosynthesis *in vitro*. The latter observations suggest that the "malic" enzyme, acting in conjunction with illuminated chloroplasts, also catalyzes net carbon dioxide assimilation in living plant cells. Yields of malate and photochemical efficiencies *in vitro* have been low, however, and the concentrations of triphosphopyridine nucleotide (T.P.N.) which have been used in the model systems have been much higher than those which have been observed in leaves (1, 39). Nonphotosynthetic organs such as pigeon liver, parsley root, and wheat germ also have been the favored sources of β-carboxylases. The role of the "malic" enzyme and other carboxylases in photosynthesis has accordingly remained unsettled.

Vennesland (30) recently reported the presence of oxalacetic carboxylase in

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cell-free extracts of market spinach, but the indicated activity was much lower than was observed in parsley root extracts. Negligible pyruvic carboxylase and formic dehydrogenase activity was observed in leaf extracts by Vennesland and Felsher (31) and by Davison (10), respectively. "Malic" enzyme has been isolated from leaf cytoplasm (2, 9), but no information has been provided on its relative abundance in different parts of the plant or on its capacity in relation to the chlorophyll content or photosynthetic capacity of the source. Apart from these observations, little else has been contributed on the carboxylases of either leaves or algae.

In undertaking to provide information on this previously neglected topic, there appeared to be three criteria which might be useful in determining which of the carboxylases serve as catalysts in photosynthesis: relative abundance or enzymatic capacity in photosynthetic and nonphotosynthetic tissues, reversibility, and sensitivity to cyanide. The photosynthetic rate at saturating light intensities usually is 20 or more times greater than the respiration rate. To cope with this heavy carbon dioxide traffic, the capacity of the enzymes involved must be correspondingly high. If a particular carboxylase is always absent in extracts of leaves, or if its activity is consistently lower in extracts of leaves than in those of roots and other nonphotosynthetic tissues, then it would appear to play no part whatever in photosynthesis. Carboxylases which are only weakly reversible *in vitro* would also seem to be ruled out as catalysts of photosynthesis. The cyanide-sensitive component of photosynthesis in strong light apparently is the initial carboxylation reaction, although the evidence on this point is indirect (14, 24). Photosynthesis is strongly inhibited by 10^{-3} to 10^{-4} M hydrogen cyanide above but not below the compensation point (11, 14, 24, 36). The Hill reaction of isolated chloroplasts or the "photochemical phase" of photosynthesis also is not inhibited by cyanide; washed chloroplasts in fact are stimulated about equally by 10^{-3} M cyanide and chloride (16).

This paper reports investigations of the distribution, intracellular location, enzymatic capacity, and reversibility of carboxylases in algae, leaves, and other plant organs. All of the carboxylases which have ever been detected in plant tissue of any kind were included in this study ("malic" enzyme, oxalacetic, oxalsuccinic, pyruvic, α-ketoglutaric, and glutamic carboxylases, and formic dehydrogenase). A search also was made for amino acid carboxylases other than glutamic carboxylase, and for an enzyme capable of decarboxylating phosphoglyceric acid *in vitro*. An investigation of carbonic anhydrase in green plants has been reported elsewhere (37). With the aid of carbonic anhydrase, Hansl and Waygood (19) have determined the state in which carbon dioxide is released by the plant carboxylases dealt with in this paper.

Materials and Methods

The plants were grown in soil, mainly under glass, and the plant parts were freshly collected and chilled prior to maceration in a cold room (0°–5° C.). The undiluted cell fluid was filtered through nylon, and the chlorophyll content

and volume was recorded. The chloroplast substance was removed by centrifugation at 16,000 g. The supernatant cytoplasm was purified by fractional or total precipitation with ammonium sulphate, followed by dialysis against distilled water or 0.025 *M* phosphate, pH 7.3 (30).

Chlorella pyrenoidosa and *C. vulgaris* were grown on an Emerson–Lewis medium as in earlier work (8), and *Scenedesmus obliquus* was grown on a medium devised by Dr. E. W. Fager, Department of Chemistry, University of Chicago. Cell-free extracts were prepared by grinding concentrated cell suspensions in ice-jacketed Potter homogenizers and centrifuging off the cell walls and unbroken cells. The algal extracts were then subjected to the same purification treatment as the leaf extracts.

Activity measurements were made at the pH optimum, usually under enzyme-limited conditions. The values reported in Table I were corrected for thermostable activity, if any, and for enzyme activity without substrate or with the decarboxylation product. Enzymatic capacities were calculated as mm.^{3}CO_2/hr./ml. of original cell fluid. The carboxylase activities observed in leaves and algae also were calculated as mm.^{3} CO_2/hr./mgm. chlorophyll in the original cell fluid, or on the same basis as is used in reporting the oxygen-producing capacity of isolated chloroplasts. The decarboxylation reaction catalyzed by the "malic" enzyme was measured spectrophotometrically at 25° C. (23) and its rate was calculated from the observed formation of reduced T.P.N. (0.0532×10^{-7} moles when $\log I_0/I$ at 3400 °A. = 0.01 for 3 ml. reaction volume, $d = 1.0$ cm. (21)). The carboxylation reaction of the isolated chloroplast – "malic" enzyme model was measured manometrically at 4000 ft-c. and 10° C. (2). Oxalacetic, oxalsuccinic, pyruvic, α-ketoglutaric, and glutamic carboxylase activity measurements were made manometrically in a nitrogen atmosphere, at 30° C. unless stated otherwise. Formic dehydrogenase activities were determined at 30° C. by the Thunberg technique (10).

Oxalacetic acid was synthesized by the method of Evans *et al.* (12) and recrystallized to 95–100% purity. Barium oxalsuccinate was provided by Prof. S. Ochoa, and free oxalsuccinic acid was prepared at 0° C. according to his directions (20). The pyruvic acid had been redistilled and all other substrates were of reagent quality. T.P.N. of approximately 65% purity was provided by Prof. B. Vennesland and Dr. E. Conn, and was also obtained from the Sigma Chemical Co. The sources of the remaining organic coenzymes were: diphosphopyridine nucleotide (D.P.N.) (Sigma), thiamine pyrophosphate (Merck), pyridoxal phosphate (Bios), and biotin (Nutritional Biochemicals).

Results

"Malic" Enzyme

Direct measurement of "malic" enzyme activity in crude leaf extracts was prevented by accompanying destruction of T.P.N. After fractional precipitation and dialysis of the cytoplasmic proteins, high activities and stable end points were then observed. The "malic" enzyme was precipitated with ammonium sulphate between one-third and two-thirds of saturation. Lower

salt concentrations precipitated less than 5% of the total "malic" enzyme, and use of salt concentrations higher than two-thirds of saturation did not lead to higher recoveries. The richest source of "malic" enzyme found in this way among higher plants was the cytoplasm of parsley leaves (Table I). The observed decarboxylation capacity of "malic" enzyme from this source was similar to the oxygen-producing capacity of isolated spinach chloroplasts, expressed on the same chlorophyll basis. Parsley leaf extracts showed higher "malic" enzyme activities than the corresponding extracts of parsley roots taken from the same plants. The decarboxylation capacity of "malic" enzyme from spinach, sugar beet, Swiss chard, and wheat leaves was less than that from parsley roots, expressed on a comparable basis. Negligible "malic" enzyme activity was observed in cell-free *Chlorella* extracts.

"Malic" enzyme from both sugar beet and parsley leaves was linked with illuminated spinach chloroplast fragments to effect photosynthesis *in vitro* under conditions similar to those employed by Arnon (2). The initial photochemical activity ($Q_{O_2}^{ch}$) was 400–450 calculated on the chlorophyll in the vessels (Fig. 1). The photochemical yield of oxygen was *ca.* 20 mm.^{3}, which

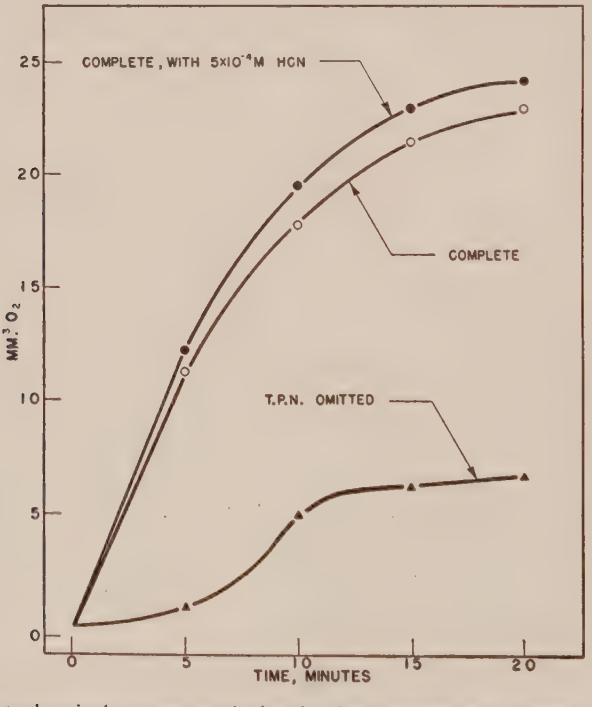

FIG. 1. Photochemical oxygen evolution in the presence and absence of cyanide by spinach chloroplast fragments linked to carbon dioxide fixation by "malic" enzyme from sugar beet leaves. Gas phase 5% carbon dioxide in nitrogen, pH 6.8. Temperature 10° C., light intensity 4000 ft-c. Complete reaction mixture: spinach chloroplast suspension (washed once) containing 0.35 mgm. chlorophyll; 20 micromoles potassium chloride; 2 micromoles manganous chloride; 100 micromoles sodium pyruvate; 0.65 micromoles T.P.N.; 21 micromoles sodium bicarbonate; 0.4 ml. "malic" enzyme solution; water or hydrogen cyanide solution to 3 ml. total volume; cyanide concentration, 5×10^{-4} *M*. Reaction started by illuminating the chloroplasts after temperature equilibration.

TABLE I

MAXIMUM "MALIC" ENZYME, OXALACETIC, AND PYRUVIC CARBOXYLASE ACTIVITIES OBSERVED ON EXTRACTS OF LEAVES AND ROOTS

Enzyme source	Pyruvic carboxylase		Oxalacetic carboxylase		Malic enzyme	
	mm.$^3CO_2$/hr./mgm. chlorophyll	mm.$^3CO_2$/hr./ml. crude extract	mm.$^3CO_2$/hr./mgm. chlorophyll	mm.$^3CO_2$/hr./ml. crude extract	mm.$^3CO_2$/hr./mgm. chlorophyll	mm.$^3CO_2$/hr./ml. crude extract
Parsley leaves	Nil	Nil	630	425	1140	1080
Parsley roots	—	1300	—	125	—	280
Sugar beet leaves	60	60	250	250	210	155
Swiss chard leaves	90	50	Nil	Nil	180	110
Spinach leaves	35	25	230	165	205	155
Wheat leaves	30	35	90	110	55	60
Kalanchoe leaves	40	65	105	165	—	—

is also in agreement with Arnon's data (2). Conn *et al.* (9) have used cyanide to inhibit catalase in their manometric yellow enzyme – "malic" enzyme test system, apparently without inhibiting the "malic" enzyme which was present in relatively high concentration. Under our conditions, the chloroplast – "malic" enzyme model was not inhibited by 5×10^{-4} *M* hydrogen cyanide, a concentration which inhibits normal photosynthesis in saturating light by more than 80% (Fig. 1). Using similar amounts of "malic" enzyme, the reverse decarboxylation reaction was not inhibited appreciably by the same concentration of cyanide. Since pyruvate forms a cyanohydrin (17), the possible removal of free cyanide by this means was investigated. Glutamic carboxylase from wheat leaves is very strongly inhibited by cyanide (Fig. 7), and was therefore used to test for effective cyanide in the presence of pyruvate. Wheat glutamic carboxylase was inhibited to the same extent by $1–2 \times 10^{-5}$ *M* hydrogen cyanide in the presence and absence of 0.003 *M* pyruvate. Use of high pyruvate concentrations was prevented by its inhibiting action on the glutamic carboxylase system (38).

Upon reducing the quantity of "malic" enzyme 20-fold, the decarboxylation reaction was then inhibited by 5×10^{-4} *M* hydrogen cyanide. Defining a unit of "malic" enzyme activity as that amount which produces reduced

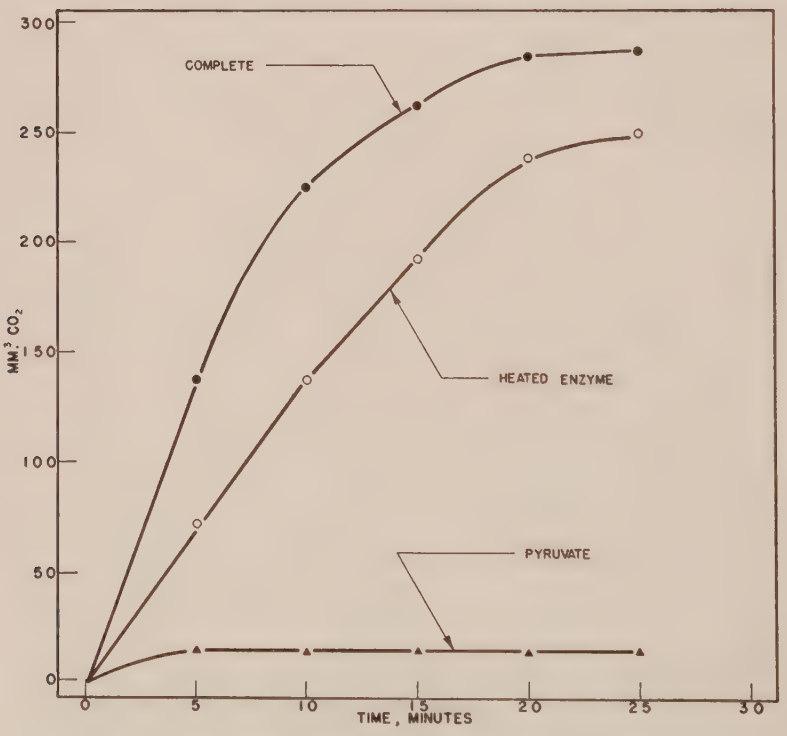

FIG. 2. Oxalacetic carboxylase activity in parsley leaf cytoplasm. 0.5 ml. 0.4 *M* acetate, pH 5.0; 0.5 ml. salt-precipitated and dialyzed enzyme solution; 0.2 ml. oxalacetic acid solution (280 μliters CO_2) or 0.2 ml. pyruvate (224 μliters CO_2); 0.1 ml. 0.2 *M* $MnCl_2$; 0.7 ml. water; N_2 gas phase, 30° C.

T.P.N. at the rate of log $I_0/I = 0.01$/min. under enzyme limited conditions at 25° C. (23), in the presence of one to five units of "malic" enzyme, there was 50% inhibition by cyanide during the first two minutes of the reaction and 20–40% during the succeeding five minutes. In manometric and spectrophotometric measurements in which no inhibition by cyanide was observed, 40 to 80 units of "malic" enzyme was employed in the 3 ml. reaction mixture.

Oxalacetic Carboxylase

Until quite recently, this enzyme was believed to catalyze the original Wood–Werkman reaction. Now its physiological function is less certain (22). Cucurbit seeds were the first plant organs in which this enzyme was demonstrated (31), and in our experience, dialyzed cucurbit seed protein has shown consistently high oxalacetic carboxylase activities. Vennesland (30) recently detected this enzyme in purified and concentrated extracts of spinach, but the observed level of activity was very much lower than for the parsley root and other nonphotosynthetic sources.

The relative abundance of this enzyme was investigated in purified extracts of parsley leaves and roots from the same plants. After purification of the cell fluid with acetate (33) or by ammonium sulphate precipitation (30), followed

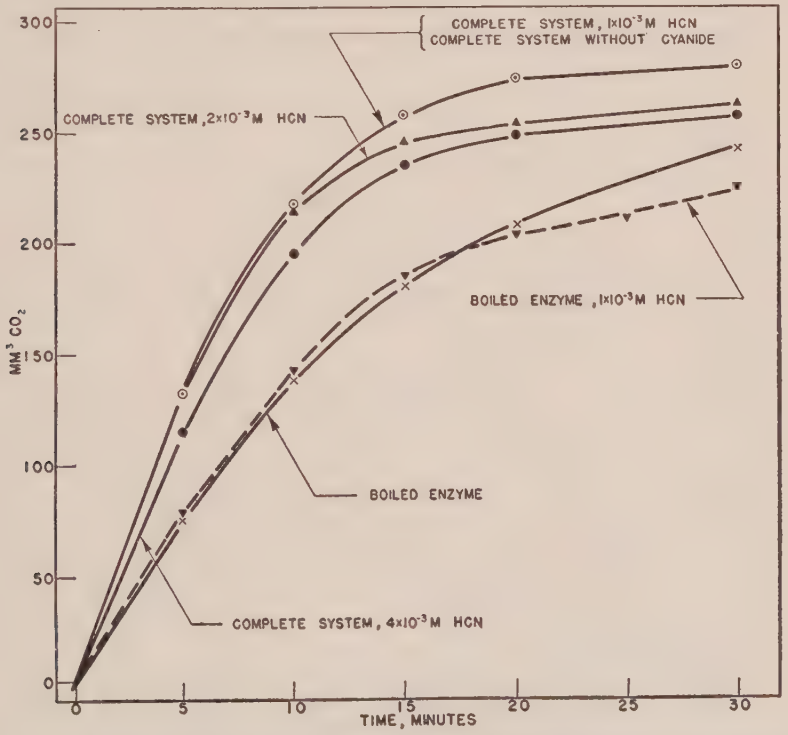

FIG. 3. Oxalacetic carboxylase activity in parsley leaf cytoplasm in presence and absence of hydrogen cyanide. 0.5 ml. 0.2 *M* acetate, pH 5.6; 0.2 ml. oxalacetic acid (280 μliters CO_2); 0.5 ml. salt-precipitated and dialyzed parsley leaf cytoplasm solution; 0.1 ml. 0.2 *M* $MnCl_2$; water or hydrogen chloride solution to 2.0 ml.; N_2 gas phase, 30° C.

by adjustment to the original volume of expressed cell fluid, there was insufficient oxalacetic carboxylase in 1-ml. aliquots for satisfactory demonstration of its presence: with heated and unheated enzyme the β-decarboxylation rates were nearly the same. This result was also obtained with the original cell fluid. The corresponding photosynthetic capacity for the same quantity of leaf cell fluid *in vivo* would be *ca.* 4000–8000 μliters CO_2/hr. (40).

Oxalacetic carboxylase was readily demonstrable in our parsley leaf and root preparations only when the cytoplasm fraction was concentrated 5-to 10-fold by salt precipitation and dialysis as a concentrated solution. Using this technique, oxalacetic carboxylase was shown to be present in the parsley leaf (Fig. 2) as well as the root, and to be absent in the chloroplast fraction. In all of the parsley populations studied, the leaf has been the richer source of this enzyme. Oxalacetic carboxylase was also found in the cytoplasm of wheat, sugar beet, Swiss chard, and Kalanchoe leaves (Table I), and weak activity was observed in extracts of *Chlorella* and *Scenedesmus*. Oxalacetic carboxylase was not detected in extracts of N.Z. spinach and barley leaves. Under the conditions used to demonstrate the presence of oxalacetic carboxylase, there was no evidence of inhibition by 10^{-3} *M* hydrogen cyanide (Fig. 3). Higher concentrations of cyanide reduced the yield of carbon dioxide, owing

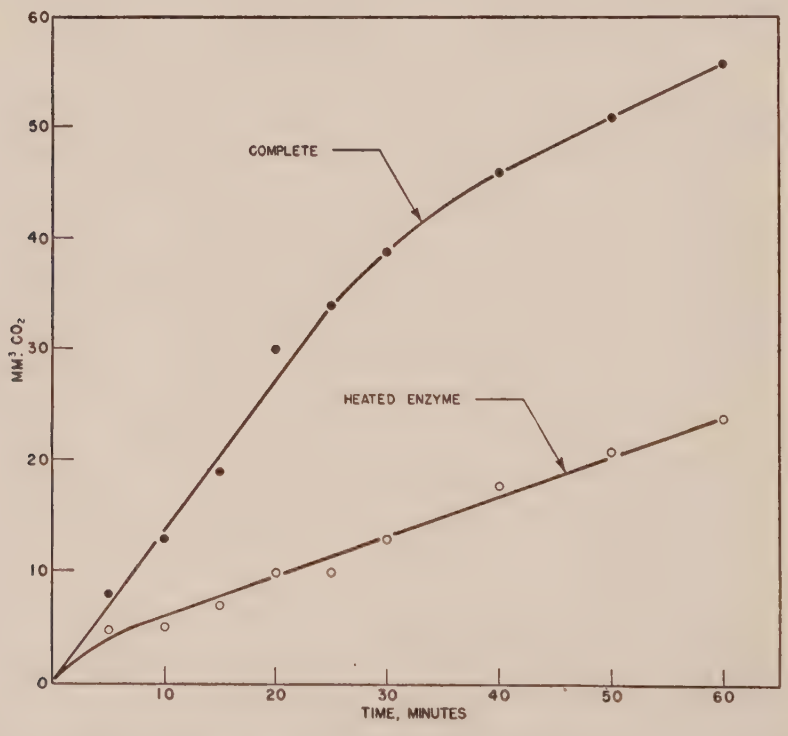

FIG. 4. Oxalsuccinic carboxylase in cytoplasm of sugar beet leaves. 0.5 ml. 0.2 *M* acetate, pH 5.6; 0.5 ml. oxalsuccinic acid solution (70 μliters CO_2); 0.2 ml. cytoplasmic protein solution; 0.1 ml. 0.02 *M* $MnCl_2$; water to 2.0 ml.; N_2 gas phase, 10° C.

to cyanohydrin formation (17). Oxalacetic carboxylase activity in parsley leaf preparations was not affected by the anion introduced with the manganese coenzyme, and also was not stimulated by biotin.

Oxalsuccinic Carboxylase

This enzyme, originally discovered in animal tissue and recently found in the parsley root (32), has not previously been demonstrated in leaves. Employing totally precipitated and dialyzed cytoplasmic protein, oxalsuccinic carboxylase was observed in extracts of both parsley leaves and parsley roots. The initial activity was *ca.* 100 μliters CO_2 per ml. original cell fluid in both cases. It could not be detected in the chloroplast fraction. Oxalsuccinic carboxylase is quite abundant in the sugar beet leaf (Fig. 4) as well as in the parsley leaf (Fig. 5). This enzyme was observed to be insensitive to 10^{-3} *M* cyanide (Fig. 5). A nitrogen atmosphere was essential in these experiments, since a rapid uptake of oxygen otherwise occurred. Oxygen uptake in air was reduced to the low endogenous rate (enzyme without substrate) on substituting α-ketoglutarate for oxalsuccinate.

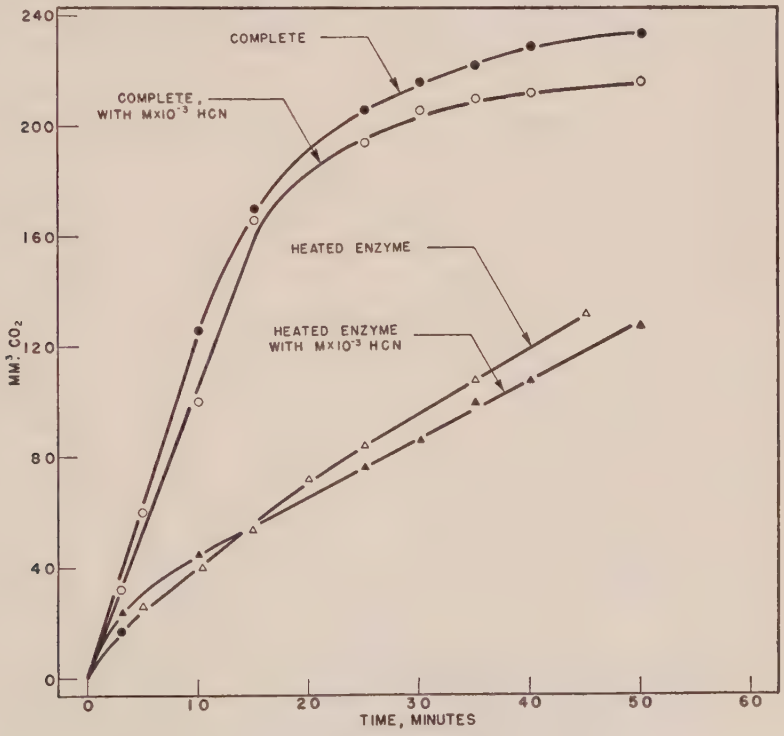

FIG. 5. Oxalsuccinic carboxylase activity of parsley leaf cytoplasm in the presence and absence of 10^{-3} *M* hydrogen cyanide. 0.5 ml. 0.2 *M* acetate, pH 5.6; 0.5 ml. oxalsuccinic acid (240 μliters CO_2); 0.5 ml. salt-precipitated and dialyzed parsley leaf cytoplasm solution; 0.1 ml. 0.02 *M* $MnCl_2$, water or hydrogen cyanide solution to 2.0 ml. Cyanide concentration 1×10^{-3} *M*; N_2 gas phase, 10° C

Pyruvic Carboxylase

Extracts of all of the leaves (Table I) and algae which were included in this study have shown either low or negligible pyruvic carboxylase activities. The capacity for oxidative decarboxylation of pyruvate was also low in both leaf and algal extracts. Although pyruvic carboxylase is abundant in extracts of parsley and radish roots, leaf extracts from the same plants showed consistently lower activities. The low pyruvic carboxylase activity of extracts prepared from photosynthetic cells was not caused by a lack of cocarboxylase, or by the presence of natural inhibitors, i.e., addition of leaf extract to an equal volume of root extract did not depress the pyruvic carboxylase activity of the latter.

A search for an enzyme or combination of enzymes capable of decarboxylating phosphoglyceric acid *in vitro* yielded consistently negative results on both crude and purified extracts of leaves and algae. Tests were conducted over a range of pH values (pH 5–7) in a nitrogen atmosphere. The rapid tagging of phosphoglyceric acid which occurs when leaves and algae are exposed briefly to $C^{14}O_2$ (5, 6, 13) thus is not catalyzed by a reversible enzyme system which retains detectable activity *in vitro*.

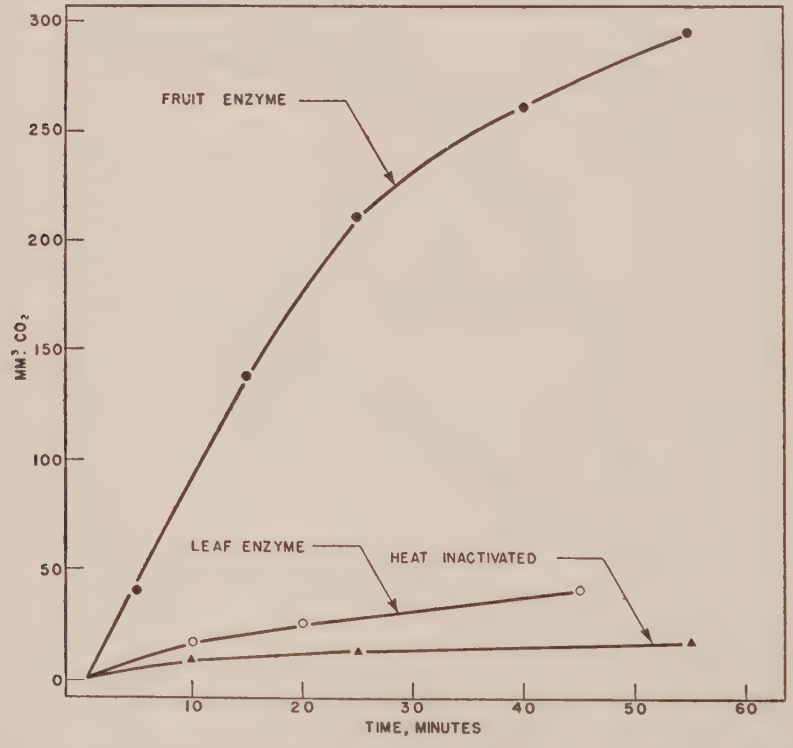

FIG. 6. Decarboxylation of α-ketoglutarate by extracts from the leaves and fruits of Hubbard squash. 0.5 ml. 0.2 *M* phosphate, pH 6.0; 0.1 ml. 1% α-ketoglutarate solution; 1.4 ml. enzyme solution (supernatant of centrifuged juice); N_2 gas phase, 30° C.

α-Ketoglutaric Carboxylase

This enzyme has been isolated previously from fruits and potato tubers (27) but has not been observed in leaf extracts. The rate of carbon dioxide production by Hubbard squash leaf cytoplasm was the same in the presence and absence of α-ketoglutarate (Fig. 6). The corresponding fruit extracts showed a high content of this enzyme, which is insensitive to cyanide and is located in the cytoplasm. α-Ketoglutaric carboxylase could not be detected in extracts of *Chlorella pyrenoidosa*, but was present in traces in extracts of *Scenedesmus*.

Glutamic Carboxylase

Schales and Schales (26) have reported that glutamic carboxylase is the only amino acid carboxylase which is present in extracts of the squash fruit. Glutamic carboxylase has also been isolated from carrots (25) and barley roots (4).

Appreciable glutamic carboxylase activity was not detected in cell-free extracts either of *Chlorella* or *Scenedesmus* or of leaves representing several species (parsley, barley, Swiss chard, spinach, New Zealand spinach, buckwheat, pea, and Kalanchoe). Glutamic carboxylase however was abundant in cell-free cytoplasm from mature wheat leaves ($Q^{ch}_{CO_2}$ = 335–1480) and sugar beet leaves ($Q^{ch}_{CO_2}$ = 120). Low activities were also observed in extracts of

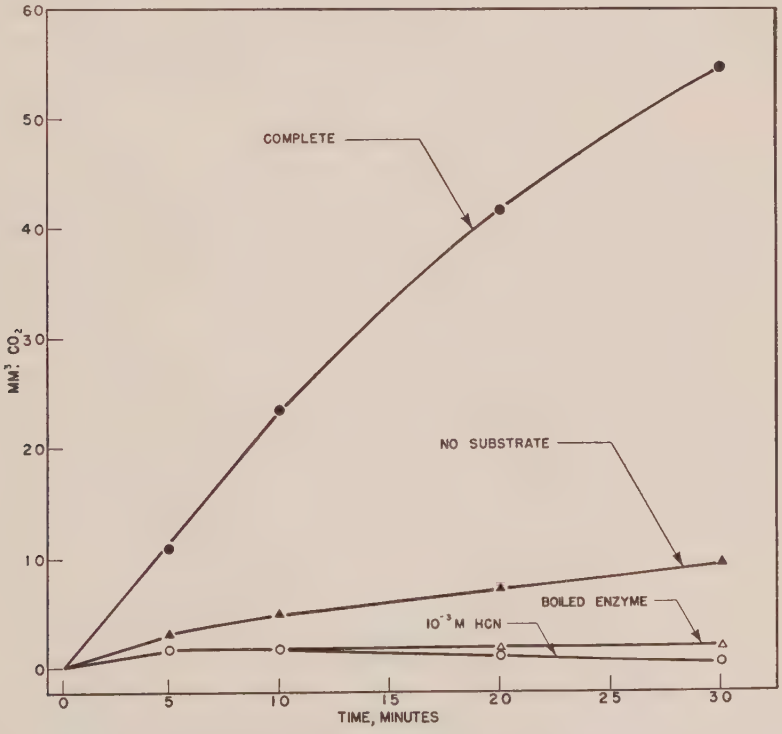

FIG. 7. Inhibition of glutamic carboxylase from wheat leaf cytoplasm by 10^{-3} *M* cyanide. 1.0 ml 0.2 *M* phosphate, pH 5.5; 10 μmoles sodium glutamate; 0.5 ml. enzyme solution; water or cyanide solution to 2.0 ml. N_2 gas phase, 30° C.

millet, oat, and flax leaves (38). Glutamic carboxylase is completely inhibited by 10^{-3} *M* hydrogen cyanide (Fig. 7). After salt precipitation and dialysis, this wheat leaf enzyme is stimulated by pyridoxal phosphate, in agreement with Schales' observations on glutamic carboxylase from carrots (25). Our tests for the presence of other amino acid carboxylases in leaf extracts (alanine, glycine, serine, aspartic acid) yielded consistently negative results.

The degree of reversibility of glutamic carboxylase has not previously been investigated. We have used the enzyme from both wheat leaves and carrot roots in such studies, employing a tracer technique similar to that which was employed in a corresponding study of bacterial lysine and tyrosine carboxylases (18). The plant enzyme was allowed to decarboxylate 20 micromoles unlabelled glutamic acid to 50% of completion, in the presence of 2×10^6 c.p.m. $C^{14}O_2$. The enzyme was then heated, free $C^{14}O_2$ was completely removed by exhaustive gassing, fresh enzyme was added and the $C^{14}O_2$ liberated from the remaining substrate was recovered as barium carbonate. A very low degree of reversibility was observed (*ca.* 200 p.p.m. fixation) similar to that which was observed recently on bacterial lysine and tyrosine carboxylases (18).

Formic Dehydrogenase

In agreement with Davison (10), formic dehydrogenase was found to be abundant in pea seeds, and to disappear completely from the seedlings a few days after germination or before photosynthesis had commenced. Formic dehydrogenase was not detected in either crude or purified extracts of leaves and unicellular algae, of which a large number were examined.

Discussion

Extracts of the unicellular algae showed low oxalacetic and α-ketoglutaric carboxylase activities, but "malic" enzyme, formic dehydrogenase, pyruvic carboxylase, and glutamic carboxylase activity was either very weak or absent altogether. The tough cell walls and small cell size necessitated a more severe grinding treatment than was required for leaves, which may have destroyed enzymes which were originally present. Cell-free extracts of *Chlorella* prepared in the same manner have previously been observed to be a poor source of photochemically active chloroplast fragments (8).

Among the seven known plant carboxylases, all of which are cytoplasmic or water soluble, at least four can be excluded as possible catalysts of photosynthetic carbon dioxide assimilation on the basis of enzyme studies. Formic dehydrogenase is abundant in seed extracts, but was not detected in extracts of leaves or algae. Pyruvic and α-ketoglutaric carboxylase activity is much lower in extracts of leaves than of roots or fruits from the same plants. Glutamic carboxylase activity was quite high in extracts of wheat leaves, and in common with formic dehydrogenase this enzyme was strongly inhibited by cyanide. Its infrequent presence in leaves and its weak reversibility indicate that it plays no part in photosynthesis. Formic dehydrogenase, pyruvic, and α-ketoglutaric carboxylases are also only weakly reversible *in vitro*. The enzymatic evidence on these four enzymes is in agreement with the reported

distributions of assimilated C^{14} in briefly exposed plants. Labelled formate, pyruvate, and α-ketoglutarate have not been identified as early products of photosynthesis (3, 5, 6). The previous conclusion that the rapid labelling of amino acids (e.g. glycine, alanine, aspartic) proceeds by amination of labelled N-free organic acids rather than by direct carboxylation with $C^{14}O_2$ is supported by the observation that glutamic carboxylase is the only amino acid carboxylase which can be detected in plant extracts, and that this enzyme is only weakly reversible. Glutamic acid is labelled rather slowly in plants exposed to $C^{14}O_2$, and a higher percentage of the assimilated C^{14} is recovered in glutamic acid after dark than after photosynthetic exposures (5).

Oxalacetic carboxylase was more abundant in extracts of mature parsley leaves than of the corresponding roots, and was found in the majority of the purified and concentrated leaf extracts which were examined. The high rates of autodecarboxylation of oxalacetic and oxalsuccinic acids and the low content of the corresponding carboxylases in the leaf extracts necessitated the use of large amounts of purified cytoplasm in demonstrating the presence of these enzymes. Although these two enzymes are reversible, they are believed to serve only minor roles as catalysts of photosynthetic carbon dioxide fixation on the basis of the present and earlier evidence. The synthesis of malate from pyruvate may now be attributed to the 'malic' enzyme rather than to linked catalyses by oxalacetic carboxylase and malic dehydrogenase. The tricarboxylic acids, oxalsuccinate and isocitrate, whose formation from α-ketoglutarate is catalyzed by oxalsuccinic carboxylase have not been identified as early products of photosynthesis (5).

Only the "malic" enzyme has shown the combination of attributes expected of a carboxylase which catalyzes photosynthetic carbon dioxide fixation. It was more abundant in extracts of mature parsley leaves than of roots from the same plants. 'Malic' enzyme from both parsley and sugar beet leaves has been linked with isolated chloroplasts to effect photosynthetic carbon dioxide fixation *in vitro*. Although insensitive to cyanide at the enzyme concentrations employed in the model photosynthesis system, "malic" enzyme from both sugar beet and parsley leaves was inhibited by 5×10^{-4} M hydrogen cyanide at very low enzyme concentrations. The enzymatic capacity of "malic" enzyme isolated from parsley leaves, the richest plant source of this enzyme that has yet been found, is similar to the Hill reaction capacity of chloroplasts isolated from spinach leaves, which are among the best sources of "active" chloroplasts. The foregoing observations support the hypothesis that the "malic" enzyme catalyzes carbon dioxide fixation in photosynthetic as well as in heterotrophic organisms.

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References

1. Anderson, D. G. Unpublished observations.
2. Arnon, D. I. Extracellular photosynthetic reactions. Nature, 1008–1010. 1951.
3. Bassham, J. A. Benson, A. A., and Calvin, M. The path of carbon in photosynthesis. VIII. The role of malic acid. J. Biol. Chem. 185 : 781–787. 1950.
4. Beevers, H. An *l*-glutamic decarboxylase from barley. Biochem. J. 48(2) : 132–137. 1951.
5. Benson, A. A. and Calvin, M. The path of carbon in photosynthesis. VII. Respiration and photosynthesis. J. Exptl. Botany, 1(1) : 63–68. 1950.
6. Calvin, M., Bassham, J. A., and Benson, A. A. Chemical transformations of carbon in photosynthesis. Federation Proc. 9 : 524–533. 1950.
7. Ceithaml, J. and Vennesland, B. The synthesis of tricarboxylic acids by carbon dioxide fixation in parsley root preparations. J. Biol. Chem. 178 : 133–143. 1949.
8. Clendenning, K. A. and Gorham, P. R. Photochemical activity of chloroplasts in relation to source and previous history. Can. J. Research, C, 28 : 114–139. 1950.
9. Conn, E., Vennesland, B., and Kraemer, L. M. Distribution of a triphosphopyridine nucleotide specific enzyme catalysing the reversible oxidative decarboxylation of malic acid in higher plants. Arch. Biochem. 23 : 179–197. 1949.
10. Davison, D. C. Distribution of formic and alcoholic dehydrogenases in the higher plants, their variation in the pea plant during its life cycle. Proc. Linnean Soc. N.S. Wales, 74 : 26–36. 1949.
11. Emerson, R. and Arnold, W. A separation of the reactions in photosynthesis by means of intermittent light. J. Gen. Physiol. 15 : 391–420. 1932.
12. Evans, E. A., Vennesland, B., and Slotin, L. The mechanism of carbon dioxide fixation in cell free extracts of pigeon liver. J. Biol. Chem. 147 : 771–784. 1943.
13. Fager, E. W., Rosenberg, J. L., and Gaffron, H. Intermediates in photosynthesis. Federation Proc. 9 : 535–542. 1950.
14. Gaffron, H. and Rieke, F. F. Flash saturation and reaction periods in photosynthesis. J. Phys. Chem. 47 : 299–307. 1943.
15. Gollub, M. C. and Vennesland, B. Fixation of carbon dioxide by a plant oxalacetate carboxylase. J. Biol. Chem. 169 : 233–236. 1947.
16. Gorham, P. R. and Clendenning, K. A. Anionic stimulation of the Hill reaction in isolated chloroplasts. Arch. Biochem. and Biophys. (In press.) 1952.
17. Green, D. E. and Williamson, S. Pyruvic and oxaloacetic cyanohydrins. Biochem. J. 31 : 617–618. 1937.
18. Hanke, M. E. and Siddiqi, M. S. H. Fixation of radio-active carbon dioxide in lysine and tyrosine by decarboxylase enzymes of these amino acids. Federation Proc. 9 : 181. 1950.
19. Hansl, N. and Waygood, E. R. Kinetic studies of plant decarboxylases and carbonic anhydrase. Can. J. Botany, 30 : 306–317. 1952.
20. Ochoa, S. Biosynthesis of tricarboxylic acids by carbon dioxide fixation. I. The preparation and properties of oxalosuccinic acid. J. Biol. Chem. 174 : 115–122. 1948.
21. Ochoa, S. Biosynthesis of tricarboxylic acids by carbon dioxide fixation. III. Enzymatic mechanisms. J. Biol. Chem. 174 : 133–157. 1948.
22. Ochoa, S. Biological mechanisms of carboxylation and decarboxylation. Physiol. Revs. 31 : 56–106. 1951.
23. Ochoa, S., Mehler, A. H., and Kornberg, A. Reversible oxidative decarboxylation of malic acid. J. Biol. Chem. 167 : 871–872. 1947.
24. Rabinowitch, E. I. Photosynthesis and related processes. Vol. 1. Interscience Publishers, Inc., New York. 1945. p. 308.
25. Schales, O., Mims, V., and Schales, S. S. Glutamic acid decarboxylase of higher plants. I. Distribution; preparation of clear solutions; nature of prosthetic group. Arch. Biochem. 10 : 455-465. 1946.
26. Schales, O. and Schales, S. S. Glutamic acid decarboxylase of higher plants. III. Enzymatic determination of *l*(+)-glutamic acid. Arch. Biochem. 11 :445-450. 1946.

27. SCHALES, O., SCHALES, S. S., and SCHWARZENBACH, G. M. α-Ketoglutaric acid carboxylase in higher plants. Federation Proc. 9(1) : 223–231. 1950.

28. TOLMACH, L. J. Effects of triphosphopyridine nucleotide upon oxygen evolution and carbon dioxide fixation by illuminated chloroplasts. Nature, 167 : 946–948. 1951.

29. TOLMACH, L. J. The influence of triphosphopyridine nucleotide and other physiological substances upon oxygen evolution from illuminated chloroplasts. Arch. Biochem. and Biophys. 33 : 120–141. 1951.

30. VENNESLAND, B. The β-carboxylases of plants. II. The distribution of oxalacetic carboxylase in plant tissues. J. Biol. Chem. 178 : 591–597. 1949.

31. VENNESLAND, B. and FELSHER, R. Z. Oxalacetic and pyruvic carboxylases in some dicotyledonous plants. Arch. Biochem. 11 : 279–306. 1946.

32. VENNESLAND, B., CEITHAML, J., and GOLLUB, M. C. The fixation of carbon dioxide in a plant tricarboxylic acid system. J. Biol. Chem. 171 : 445–446. 1947.

33. VENNESLAND, B., GOLLUB, M. C., and SPECK, J. F. The β-carboxylases of plants. I. Some properties of oxalacetic carboxylase and its quantitative assay. J. Biol. Chem. 178 : 301–314. 1949.

34. VISHNIAC, W. and OCHOA, S. Photochemical reduction of pyridine nucleotides by spinach grana and coupled carbon dioxide fixation. Nature, 167 : 768–769. 1951.

35. VISHNIAC, W. and OCHOA, S. Fixation of carbon dioxide coupled to photochemical reduction of pyridine, nucleotides by chloroplast preparations. J. Biol. Chem. 195: 75-93. 1952.

36. WARBURG, O. Uber die Geschwindigkeit der photochemischen Kohlensäurersetzung in lebenen Zellen. Biochem. Z. 103 : 188–217. 1920.

37. WAYGOOD, E. R. and CLENDENNING, K. A. Carbonic anhydrase in green plants. Can. J. Botany, C, 28 : 673–689. 1950.

38. WEINBERGER, P. and CLENDENNING, K. A. Glutamic carboxylase of the mature wheat leaf. Can. J. Botany. In press. 1952.

39. WHATLEY, F. R. Coenzymes in plants. New Phytologist, 50 : 244–257. 1951.

40. WILLSTATTER, H. and STOLL, A. Untersuchungen uber die assimilation der Kohlensaure. Julius Springer, Berlin. 1918.

41. WOOD, H. G. The fixation of carbon dioxide and the interrelationships of the tricarboxylic acid cycle. Physiol. Revs. 26 : 198–246. 1946.

A STUDY OF THE SPECIES OF *CINTRACTIA* ON *CAREX*, *KOBRESIA*, AND *SCIRPUS* IN NORTH AMERICA[1]

By D. B. O. Savile[2]

Abstract

This is a taxonomic study of *Cintractia* spp. on nearly one hundred host species, mainly in Canada, northern United States, and southern Alaska. Coverage is very incomplete for northern Alaska, Greenland, and parts of the Canadian arctic archipelago. Eighteen species and varieties are recognized including one new species, *Cint. atratae*, and four new varieties, *Cint. carpophila* vars. *kenaica* and *verrucosa* and *Cint. caricis* vars. *intermedia* and *acutarum*. Two recombinations are made. The biology and phylogeny of the group are also discussed.

Introduction

In recent years botanical work in northern Canada, particularly by members of the Division of Botany and Plant Pathology, has made available abundant material of *Cintractia* spp. on *Carex*, *Kobresia*, and *Scirpus*. These smuts form a fairly natural group and represent most of the species of *Cintractia* to be found north of the United States; it is, therefore, convenient to treat them as a unit. The coverage of the present paper is not complete, but it is sufficiently full to give a reasonable picture of the species concerned, their host range, and their approximate geographic distribution. It is considered desirable to publish the findings now in order to make them available to Dr. Geo. W. Fischer for incorporation into his forthcoming treatment of the *Ustilaginales* of North America. Coverage is reasonably complete for most of southern Canada except much of British Columbia. Southern Alaska, Yukon, Mackenzie, Keewatin, Ungava, southern Baffin I., Labrador, and northern Newfoundland have been fairly adequately sampled; but there is inadequate material from northern Alaska, much of the Canadian arctic archipelago, and Greenland.

The present treatment may appear unduly complex to those accustomed to the greatly oversimplified one supplied by Clinton (3) and Zundel (13), but it is based on detailed morphology and is actually somewhat conservative. Several species recognized by European workers, largely perhaps on the basis of host relationship, are here reduced to synonymy. Furthermore it will be observed that, although a species or variety is generally based on a particular species or section of *Carex*, it has often been necessary to assign to it smuts on less closely related hosts. Some of these other smuts show small morphological differences and are probably specialized upon their own hosts. In theory they should be given varietal rank, but the material is not always adequate to confirm that the distinctions are constant, and any great amount of further splitting would make the preparation of keys and distinguishing descriptions

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almost impossible. These smuts appear, like the genus *Carex*, to be in a state of active evolution, and some species, notably *Cintractia carpophila* and *Cint. caricis*, are complexes with a multiplicity of intergrading forms.

Each year since the present study started more hosts have been added to the substantial list of those that take more than one smut. Although it is believed that most of the clearly defined species and varieties of *Cintractia* on *Carex* in North America have been encountered, it is reasonable to believe that the list of hosts is still appreciably incomplete. The reader is accordingly cautioned against too great a reliance upon the host as an aid to identification.

Biology

Ainsworth (1), in a recent review, has pointed out that taxonomy of the smuts has far outstripped natural history. In spite of the many imperfections in the taxonomy of *Cintractia*, Ainsworth's claim is unfortunately as true for this genus as for any in the order. Although of importance ecologically, the Cyperaceae are not economically very important from the agricultural standpoint, and their diseases have not received the detailed study that has been accorded to those of the Gramineae. There are various other difficulties involved, not the least being that many of the hosts would be extremely difficult to grow under artificial conditions and that they and their smuts are generally to be found far from laboratory facilities. Nevertheless there are susceptible upland species that should be simple to handle. In northern Canada, at least, much of the collecting of these smuts has been done by phanerogamic botanists; in fact the writer suspects that he is the first mycologist to collect in the Canadian arctic, and even he has worked there primarily as a phanerogamic botanist with only limited time available for mycology. Consequently even detailed field observations are extremely limited, and our ignorance of the natural history of the group is deplorable. A few observations derived both from the study of specimens and from personal observations in the arctic and subarctic may be of some value.

In moist, northern, maritime, or alpine situations it appears that an adequate search will yield smuts on nearly half the potential host species in any one year. Although few drier, inland areas have been adequately sampled, it is plain that the proportion of smutted species is generally much lower, perhaps 5–10% of the total. There is some evidence to suggest that sustained wet weather in early summer— the anthesis period for the hosts—increases the amount of infection. Mr. J. A. Calder found smuts on no less than 26 out of 45 species (58%) in the Kenai Peninsula, Alaska, in 1951, following an extremely wet early summer. By contrast the writer found only 15 out of 42 species (35%) infected at St. Anthony, Nfld., where, despite much fog, almost no rain fell from June 3 to June 25 inclusive, an exceptional situation for that coast. At Chesterfield Inlet, Keew., on the west side of Hudson Bay, in 1950, 35% of the species were infected under conditions of normal rainfall and little fog. At Great Whale River, Que., on the east coast of the bay, in 1949, 42% were infected following normal rainfall but abundant fog. There are so many

variables involved that such data are naturally far from precise; but it is reasonably certain that the figures for the Kenai Peninsula and St. Anthony are almost complete for both smuts and hosts. It is perhaps significant that *Carex aquatilis*, a marsh species that is commonly and heavily infected from coast to coast, bore very little smut at St. Anthony in 1951, only one lightly infected colony being found although the host was plentiful. In contrast, the hilltop species, *C. rupestris* and *C. scirpoidea*, which were often enveloped in fog for long periods, were so heavily infected that it was difficult to obtain adequate phanerogamic specimens. In strategic situations that are exposed to sea fog, sheltered from drying winds, or subject to splash from falling water, two or more sedges may be heavily infected by different smuts, a situation that has given rise to erroneous ideas of host range when the observation was not backed by careful morphological study of the smuts. Such associations were seen at Great Whale River between *Carex capillaris* and *C. scirpoidea* and between *C. scirpoidea* and *Scirpus caespitosus*, all of which bore distinct smuts. The writer has not collected these smuts in alpine meadows, but in favorable years infection in such areas seems to be very heavy. A note with an old collection of *Carex atrata* from Colorado that was sent to J. B. Ellis for determination is illuminating. The unknown collector wrote on the packet: "The fruit of nearly all the *Carices* above timber line is destroyed by a fungus. I suppose the fungi are all of the same species . . . ."

This point of environment has been somewhat labored because, surprisingly enough, almost nothing is definitely known about the method of infection in the genus *Cintractia*. Since he first saw heavy infection in 1949 the writer has assumed, from the field picture, that, in the species treated here, infection takes place in the florets, probably via the styles at anthesis. It came as a shock to find that it has been rather widely assumed, mainly because of some conjectures by Brefeld, that the mycelia are systemic and perennial and that the florets become infected from mycelium in the culms much as in many grass smuts. The speculations have been summarized by Liro (9, p. 233), who, with his wide field experience in the north, must have been somewhat dubious of Brefeld's conclusions. It is, of course, not certain exactly what organism Brefeld meant when he spoke of *Cintractia caricis*; it was conceivably some form distinct from any here treated.

All systemic fungi known to the writer modify the anatomy of the host to some degree, causing spindly growth, change in height, blasting of flowers or even complete suppression of flowering. This is exemplified in varying degrees by the systemic grass smuts. The systemic *Schizonella* spp. and the curious fungus ill-advisedly named *Cintractia arctica*, which is discussed later, generally completely suppress flowering. No species of *Cintractia* on *Carex*, *Kobresia*, or *Scirpus* yet seen by the writer visibly modifies any part of the host plant other than the infected florets. This fact is not always evident from mycological specimens, which too frequently consist of mere scraps of the inflorescence. During the last four years the writer has scrutinized some two thousand phanerogamic collections of *Carex*, ranging up to over fifty sheets apiece, of

which several hundred were infected. This examination, together with three summers' observations in northern maritime areas, enables him to state with some assurance that no evidence can be found to support the suggestion that any of the floret-infecting species on these host genera are systemic. The species attacking *Juncus* and *Luzula*, which have not been seen in the field by the writer, seem sometimes to affect the host severely and may be in a different category. It is true that culms of *Carex* may occasionally be found with all or almost all pistillate florets infected, but in the same colony infection ranges gradually down to light or nil. Heavily infected centers are seen in the colony, from which infection decreases radially. One does not find completely healthy and completely infected plants side by side without intergradation, as happens with systemic infection. There is no regular pattern in the distribution of infected florets in the inflorescence. They may be mainly basal, mainly apical or, as is most usual, randomly scattered. On plants with several pistillate spikes, infection is sometimes heaviest on the lower and sometimes on the upper spikes, probably depending on the weather at the time when the florets were in the receptive stage.

Ecological data will often add to our knowledge of the biology of the group. With hosts of saline habitats it is of interest to know whether the plants are ever reached by the tide. Limited data suggest that the smuts of *Carex salina* can persist only beyond the reach of the tide, perhaps because of the problem of spore survival during the winter. It is also desirable to note whether adjacent sedges are smutted. For example, *Carex buxbaumii*, which generally takes a different smut, bore a trace infection, at St. Anthony, of the smut that was affecting contiguous *C. aquatilis*.

There is a distinct suggestion in *Cintractia limosa*, which is here treated as three varieties on the basis of spore size, that on the Atlantic and Pacific coasts the spores are larger on some hosts than in the interior or even on the Hudson Bay coast. This point will be evident when the host distribution for each variety is studied. The explanation of this tendency is not known. It may be physiological, but it is also just possible that it is genetic. If large spore size were recessive it might be expected to show up most frequently at the periphery of the range where closer breeding would presumably occur. A similar explanation may hold for the conspicuous predominance of melanistic forms of some rodents at the edge of the range. The same tendency for large spores to occur on both coasts has been noted by the writer in the rusts *Chrysomyxa empetri* and *C. ledicola*. Whatever the explanation may be, the phenomenon indicates that caution must be used in segregating forms on the basis of spore size alone.

Methods of Study

The supposition quoted above from the anonymous collector in Colorado has unfortunately been duplicated by many mycologists. The occurrence of several species of *Cintractia* in an area favorable to both hosts and parasites tends to favor a belief that they are all the same although the alternative

explanation is equally logical. Thus Linder (8, p. 268) refers to the finding of smuts on *Carex glacialis*, *C. misandra*, *C. nardina*, *C. rupestris*, and *Kobresia simpliciuscula* within a few days at Lake Harbour, southern Baffin I., as evidence that they were a single organism. Actually these five sedges take five morphologically distinct smuts as will be shown below. Admittedly a certain amount of lumping in the difficult complexes referred to earlier seems necessary if one is to achieve a usable classification; but to disregard the manifold distinctions between many forms by putting them all together renders impossible any appreciation of the phylogeny of the parasites in relation to that of their hosts and also hides the fact that many sedges take two or more smuts.

It is apparent that a fully satisfactory classification of this interesting complex will require the best of methods and materials. The following suggestions are made in the hope that they will help to bring about such an improvement.

Many more specimens are needed on some hosts and from several areas, but they must meet certain requirements. In dealing with parasites of a genus as complex as *Carex* it is essential that every collection should be accompanied by intact plants, for host identification may be difficult enough with good specimens and impossible without them. Many small arctic or alpine sedges will fit into a packet of normal size, but this is not true of most southern species. If complete plants are put in the packets they should be cleaned well; otherwise soil particles are often transferred to the mount and prevent the cover slip from falling into place. If adequate specimens cannot be included in the packet, a phanerogamic reference sheet must be made. The writer makes it a rule to take a phanerogamic specimen under the same collection number as that given to the smut, even when intact plants are included in the packet. Thus if there is a revision of host identification at any time it is a simple matter to enter the change on the smut specimen and its index card. This point of adequate host specimens cannot be stressed too strongly, for both Mr. Calder and the writer have spent many hours puzzling over fragments that clearly were not what they purported to be. It is hoped that host errors in the present treatment have been held to the minimum, but it is probable that they are not entirely absent. No precise record has been kept of misdetermined hosts, but the percentage is known to have been disturbingly high in specimens from various sources. Some hosts are listed below with a question mark if the specimen is of any interest; but several have had to be deleted because even approximate determination could not be made. A question mark against the locality indicates doubt as to the host identity for that locality. It is generally advisable to collect from several colonies of a host in any area, for more than once a sedge has been found to harbor two smuts within a mile or two. The desirability of including pertinent ecological data has already been emphasized.

The basis of spore descriptions adopted here must be clearly understood. Linder (8) speculated of *Cintractia caricis*, in his sense, that "by the application

of culture studies and biometrics, this species may be broken down into varieties or races . . . . ." Needless to say, anything approaching a complete cultural and inoculation study is out of the question because of the inaccessibility of most of the material. The biometrical approach is tedious at best and is of doubtful value since it is too cumbersome to apply to any characters other than spore dimensions. It has been used with moderate success by Lehtola (7) in conjunction with other approaches; but it proved disastrous in the hands of Ciferri (2) whose data not only placed together forms whose only resemblance was in approximate over-all size but even showed apparent differences where none existed. For the present we must rely largely on morphological distinctions. Actually there are so many good morphological characters available that if we make the fullest use of all of them most of the forms can be grouped fairly naturally according to host section, subsection, or species. One of the more encouraging aspects of this work has been that examination of the smut has frequently correctly forecast the approximate identity of the host.

The characters available are the following: range of spore length; range of spore width; spore shape; range of wall thickness; spore wall color; form of warts and their range of height, width, and center-to-center spacing; and approximate number, if any, of internal swellings on walls. In general, the recommendations of the writer (11) for the study of *Chrysomyxa* spores apply to the present group. It is first necessary to appreciate that the basic spore form in the genus *Cintractia* is a flattened ellipsoid. This form is illustrated in Fig. 1, a semidiagrammatic drawing of a spore of *Cint. carpophila* in plan, end elevation, and side elevation. Thus there are theoretically three linear dimensions, length (*a*), width (*b*), and depth (*c*). In practice the orientation of the spore is often oblique or uncertain; accordingly one must use "lengths" that are approximate widths or lengths and "widths" that are approximate depths or widths. This situation may partly explain the difficulty attending a biometric approach; excessive dispersion of the spores and pressure on the cover slip will give entirely different modes from a dense mount with the cover lightly applied. Similarly the measurement of only a few spores may give anomalous results. The quickest and most satisfactory way of establishing size ranges is to search for extremes of length and width and then fill in the gaps until a smooth series results. Any seemingly exceptional dimensions are put in parentheses on the card for the specimen, and palpably malformed spores are ignored. In species with conspicuously angular spores, such as *Cint. caricis* (Fig. 6), the basic pattern is less obvious, but it is still present. It is essential to have spores in all orientations not only to obtain the full size range but because the wall is generally thinner on the flattened faces than elsewhere. In the present treatment spore walls are described as smooth if no irregularity can be seen under the 2 mm. objective and critical lighting. The walls are described as minutely roughened if irregularities are barely discernible and minutely verrucose if warts are regularly discernible but are too small for reliable measurement. Where more conspicuous decorations occur the dimen-

sions are given. The internal wall swellings are a distinctive feature of the cleared spores of some species, e.g. *Cint. carpophila* (Fig. 1). They are commonly about 0.5 μ high and are visible as circular dark spots in surface view. They are less easily seen in angular spores with irregularly thickened walls. These swellings seem to originate at points of contact between the immature spores in the sorus. It is questionable whether they have any biological function, but they do have some taxonomic value. Spore dimensions are inclusive of warts; but wall thicknesses are exclusive of warts and internal swellings although inclusive of the ridged portions of angular spores (Fig. 6). Wall color is of limited value, since it depends to a considerable extent on illumination. All colors given refer to spores thoroughly cleared by boiling in lactophenol. Mounts are made by placing spores, preferably from about three sori, in a very small drop of lactophenol with copious lactophenol streaks on either side. When the cover is lightly applied the fluid displaces most of the air but leaves the spores closely congregated at the center. With a little practice all air may be boiled out over a small flame without dispersing the spores. The cover is then depressed and oscillated under the dissecting microscope just enough to give a satisfactory spacing of the spores.

The illustrations (Figs. 1–6) are semidiagrammatic plan views of representative spores of six well-defined species, chosen to show the main variations in spore characters. Many intermediates occur, and the variability in a single specimen is sometimes such that several spores would be required to illustrate it adequately. More reliance is to be placed upon full descriptions and reference specimens than upon illustrations.

In denoting distributions, the records are given by states, provinces, or districts from north to south and west to east rather than alphabetically under countries, in order to simplify the visualization of ranges. The districts of Franklin, Keewatin, and Mackenzie, of the Northwest Territories, are abbreviated to "Frank.", "Keew." and "Mack." "Nfld." refers only to the island portion of Newfoundland and "Labr." to the Newfoundland Labrador. The adjoining areas, sometimes termed Quebec Labrador, are listed under Quebec.

In the difficult matter of delimiting host species no single system has been followed in full. A large proportion of names will be found to comply with the usage of Fernald (4), but some departures have been made, particularly with northern species, on the advice of specialists. Many variety names have been omitted from the host lists for several reasons. In some instances the species concerned are in need of revision and current variety names are of limited value; in others, where more than one variety of a smut is involved, the segregation of the records by host variety would unduly complicate presentation of the data. Many specimens are inadequate for delimitation beyond species. Finally, the hosts of some recent collections still require critical study although they have been identified as closely as existing treatments allow.

Taxonomy

The synonymy of most of the species concerned has been given fully in the comprehensive study of Liro. In the following treatment only such synonyms as are desirable to ensure clarity are cited.

Key to North American Species and Varieties

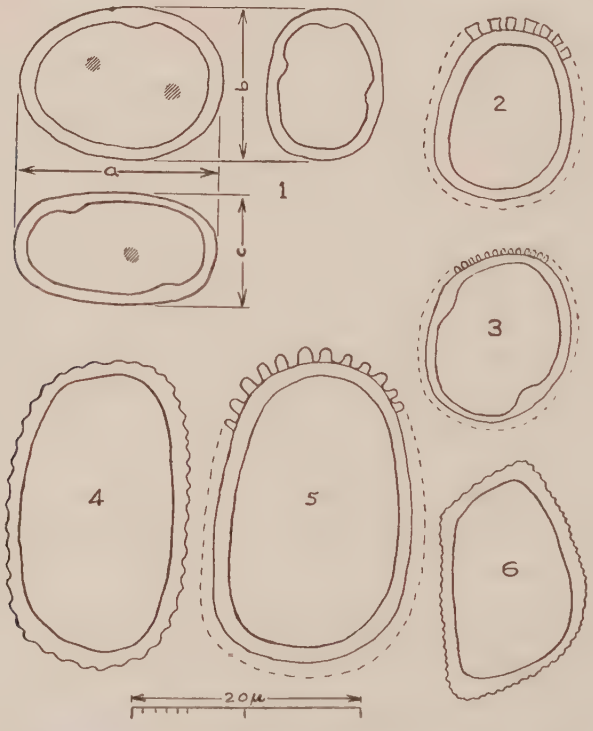
1. Spores small, 13–21 × 9–17 (20) μ, or if slightly larger (13–23 × 10.5–20 μ) then with several distinct internal swellings or with large truncate warts
   2. Spore wall smooth to finely verrucose
      3. Wall smooth to minutely verrucose
         4. Wall with definite internal swellings
            5. Spores 13–20 (22) × 9–17 μ ..... *C. carpophila* var. *carpophila*
            5. Spores 16–23 × 11.5–19.5 μ ..... *C. carpophila* var. *kenaica*
         4. Wall rarely with few shallow internal swellings ..... *C. carpophila* var. *elynae*
      3. Wall distinctly verrucose, warts *ca.* 0.2 μ high ..... *C. carpophila* var. *verrucosa*
   2. Spore wall with conspicuous warts
      6. Warts 0.3–1.0 μ high, 0.2–0.4 μ wide; wall usually with 2 internal swellings .. *C. fischeri*
      6. Warts 0.3–1.8 μ high, 0.3–1.5 μ wide; wall without internal swellings .. *C. subinclusa*

1. Spores medium, 15–25 (27) × 10–21 μ
   7. Spore wall smooth or minutely roughened
      8. Spore wall often with hyaline outer sheath; spores 16–23 μ long, excluding sheath ..... *C. externa*
      8. Spore wall without external sheath; spores 17–24 (25) μ long ..... *C. scirpi*
   7. Spore wall appreciably verrucose
      9. Warts conspicuous, more or less cylindric, (0.1) 0.3–0.6 μ high; wall 1.0–4.0 μ thick ..... *C. aspera*
      9. Warts generally lower, broadly rounded; wall 0.5–3.2 μ thick
         10. Spores frequently angular or, if mostly rounded, frequently with internal swellings
            11. Spores strongly angular; no internal swellings ..... *C. caricis* var. *caricis*
            11. Spores rounded to moderately angular; occasionally 1–2 internal swellings ..... *C. caricis* var. *intermedia*
            11. Spores rounded or rarely slightly angular; usually 1–3 internal swellings ..... *C. caricis* var. *acutarum*
         10. Spores rounded; walls without internal swellings
            12. Warts frequently elongate, producing a labyrinthiform pattern ..... *C. atratae*
            12. Warts regularly circular ..... *C. limosa* var. *minor*

1. Spores large, *ca.* 18–33 × 13–28 μ
   13. Spore wall with warts 0.1–0.4 μ high
      14. Spores rounded or rarely slightly angular; walls without internal swellings
         15. Spores 19–30 × 13–25 μ ..... *C. limosa* var. *limosa*
         15. Spores 22–33 (35) × 15–28 μ ..... *C. limosa* var. *gigantissima*
      14. Spores moderately angular; walls often with internal swellings ..... *C. pratensis*
   13. Spore wall with conspicuous warts 0.5–1.5 μ high ..... *C. calderi*

CINTRACTIA CARPOPHILA (Schum.) Liro (9, p. 27. 1938) var. CARPOPHILA
(*Uredo carpophyla* Schumacher, Enumeratio Plantarum, p. 203. 1803).
(? *Cintractia glareosa* Liro, l.c., p. 22).
(*Cintractia karii* Liro, l.c., p. 31).
(*Cintractia leioderma* (Lagerh.) Ciferri (2) p. 45. 1931).
(*Ustilago caricis β leioderma* Lagerheim, Mitteil, Badisch. Bot. Vereins, p. 37. 1888).

The following description is based on two European specimens, including Romell F. Exs. 135, on *Carex caespitosa*, the type host. Teliospores 13.0–20.5 (22.0) × 9.0–17.0 μ rounded or rarely slightly angular. Wall 0.6–1.5 μ, chestnut to blackish brown, almost smooth or with warts to about 0.1 μ high, 0.2–0.3 μ wide, 0.4–1.0 μ spacing; usually 2–3 (4) distinct internal swellings (Fig. 1). North American specimens seen that show almost no variation, except occasionally more numerous internal lobes, occur on: *Carex aenea* (Que.), *C. angustior* (Que., Nfld.), *C. atherodes* (Sask.), *C. brunnescens* (Alaska, Ont., Que., Vt., Nfld.), *C. canescens* (Alaska), *C. gynocrates* (Yukon, Que.), *C. interior* (Que.), *C. lanuginosa* (Que.), *C. loliacea* (Alaska), *C. lugens* (Yukon), *C. pauciflora* (Alaska), *C. praticola* (Yukon), *C. rossii* (Alaska, B.C.), *C. salina* var. *kattegatensis* (Que.), *C. stricta* (Ont.), *C. trisperma* (Ont.). *Cintractia*



FIGS. 1 to 6. Representative spore types of *Cintractia* spp. FIG. 1. *Cint. carpophila*; plan view (upper left), side elevation (below), and end elevation (right); showing basic spore shape; see text. FIGS. 2–6 are plan views. FIG. 2. *Cint. subinclusa*. FIG. 3. *Cint. fischeri*. FIG. 4. *Cint. limosa*. FIG. 5. *Cint. calderi*. FIG. 6. *Cint. caricis* var. *caricis*.

karii, on *Carex brunnescens*, has up to 5 or rarely 6 internal swellings in a few collections, but in the remainder the number is 2–4.

On the following hosts the internal swellings tend to be fewer, usually 1–3, but there is no distinction clear enough to warrant varietal rank: *Carex bromoides* (N.Y.), *C. disperma* (Alaska, Yukon, Alta.), *C. filifolia* (Wyo.), *C. glareosa* (Greenl.), *C. gynocrates* (Alaska, Mack., Sask., Man., Ont.), *C. leptonervia* (Nfld.), *C. marina* (Keew.), *C. nardina* (Keew.), *C. petricosa* (Alaska), *C.* ? *praegracilis* (Colo.), *C. tenuiflora* × ? *gynocrates* (Alaska), *Kobresia myosuroides* (Yukon). Two of three collections on *Carex marina* from Chesterfield Inlet and the single one from Greenland on the closely related *Carex glareosa* (described as *Cint. glareosa*) have poorly defined internal swellings and tend toward the next variety, but the material on hand is insufficient to make it clear whether Liro's species can be kept as a distinct variety. A third collection on *Carex marina* is typical of the next variety.

The smut on *Carex pauciflora* is not to be confused with *Cint. caricis–pauciflorae* Lehtola in Finland, which has much larger spores and is apparently very close to if not identical with *Cint. limosa*.

Carex filifolia is here treated in the broad sense (see under *Cint. externa*). Fragmentary and smutted plants in this group often defy precise identification. The smut cited from Wyoming approaches the next variety, and one from Colorado on a plant apparently in sect. Filifoliae definitely belongs there. Further collecting on this group of plants is needed.

CINTRACTIA CARPOPHILA (Schum.) Liro var. **elynae** (Syd.) Savile comb. nov. (*Cintractia elynae* Sydow. Ann. Mycol. 22 : 289. 1924).
(? *Cintractia kobresiae* Mundkur, Mycol. 36 : 291. 1944).

Teliospores 13.5–21.0 × 9.5–18.0 (20.0) μ, rounded. Wall 0.8–2.2 μ, chestnut to blackish brown, smooth to very finely verrucose with warts *ca.* 0.1 μ high, 0.1–0.2 μ wide, 0.4–1.0 μ spacing; at most 1–2 very shallow internal swellings, generally none.

The presence of shallow internal swellings in one collection on *K. myosuroides* and their virtual absence in one on *Carex marina*, together with the numerous similarities between the spores, indicate the advisability of reducing *Cint. elynae* to varietal rank. *Cint. kobresiae* has not been seen, but the spore size given is about that of the present organism, despite Mundkur's statement to the contrary.

Specimens on the following hosts belong here: *Carex lachenalii* (Alaska, Yukon), *C. marina* (Keew.), *C. praegracilis* (Sask., Mont., Wyo., Colo.), *Kobresia myosuroides* (Frank.), *K. simpliciuscula* (Man., Keew., Frank., Que.), European specimens on *K. myosuriodes* (*K. bellardi*) agree exactly.

CINTRACTIA CARPOPHILA (Schum.) Liro var. **kenaica** Savile var. nov.

Teliosporae 16.0–23.5 × 11.5–19.5 μ, compressae, ellipsoideae, nunquam angulater. Episporium 0.6–1.3 μ, castaneum, leve; saepius interne gibberibus 2–5 munitum.

In ovaries of *Carex pyrenaica* Wahl. ssp. *micropoda* (C. A. Meyer) Hultén: Head of Palmer Creek Valley, *ca.* 60° 49′ N.: 149° 33′ W., Kenai Peninsula,

Alaska, 26 July 1951, leg. J. A. Calder 6229 (TYPE); two other collections have been seen on this host from the Kenai Peninsula (Calder 6095, 6475). A single collection on *C. deweyana* from the same region (Calder 6397) is provisionally placed here; the spore walls are sometimes minutely roughened and the internal swellings are less conspicuous. The differences in size that are the chief distinctions of the variety are relatively small but very consistent.

CINTRACTIA CARPOPHILA (Schum.) Liro var. **verrucosa** Savile var. nov.

Teliosporae 14.5–20.0 × 9.5 × 17.0 μ, compressae, ellipsoideae, nunquam angulater. Episporium 0.6–1.4 μ, verrucis exclusis, castaneum; verrucis rotundatis (0.1) 0.2–0.3 μ alt., 0.2–0.5 (1.0) μ lat., quorum centrum a centro abest (0.3) 0.6–1.4 (1.6) μ; saepius interne gibberibus 1–2(3) munitum.

In ovaries of *Carex ebenea* Rydb. (issued as *Carex festivella*), L. Marie, Medicine Bow Mts., Wyo., 21 Aug. 1941, leg. W. G. Solheim 2009 (Myc. Saximont. Exs. 439, in herb. W. G. Solheim) (TYPE); also on *C. macloviana* ssp. *pachystachya*, Kenai Peninsula, Alaska, J. A. Calder 6409, 7034. A specimen on *C. festivella* from Anita Peak, Colo. (U. of Wyoming acc. 52463) is tentatively placed here, but lacks internal swellings. Sydow Ustil. 314 on *C. "festiva"* (presumably some species in this group of plants) may well belong here, but it has not been available for study.

This variety, well defined by its distinctly verrucose spores, is apparently restricted to plants of the subsection Festivae of the section Ovales. It may be confined to west of the continental divide, for *Carex macloviana* and its segregates and related species, although widespread, have a curiously disjunct distribution; but Hagen (5) reports what may be the same fungus from eastern Greenland on *Carex macloviana*.

CINTRACTIA FISCHERI (Karst.) Liro (9, p. 20. 1938)
(*Tilletia fischeri* Karsten, Meddel. Soc. F. F. Fenn. 2 : p. 183. 1878).
(*Cintractia inclusa* (Bref.) Liro, l.c., p. 16. 1938).
(*Anthracoidea inclusa* Brefeld, Untersuch. aus d. Gesammtg. d. Myc. 15 : pp. 36, 150. 1912).

Examination of a fragment of the type collection, on *Carex canescens*, Vasa, Finland, 9 Aug. 1867, leg. P. A. Karsten, yields the following description: Teliospores 14.0–19.5 × 10.5–17.0 μ, rounded. Wall *ca.* 0.7–1.4 μ (doubtful because of crowded warts), yellowish brown to chestnut; with prominent cylindrical round-topped warts 0.3–0.8 μ high, 0.2–0.4 μ wide, 0.5–1.2 μ spacing; commonly 2–3 small internal swellings. Liro Myc. Fenn. 105 is partly this smut and partly *Cint. carpophila*, which has also been seen on this host from Alaska and Sweden. Specimens from Kenai Peninsula, Alaska, and Garibaldi, B.C., agree closely with the type. *Cint. inclusa* on *Carex rostrata* and various other species is indistinguishable. A summary of 13 North American collections on *Carex rostrata* (Alaska, B.C., Alta., Wyo., Ont., Que.) gives the following description: Teliospores 11.0–19.5 (22.0) × 9.0–17.5 (20.0) μ, rounded. Wall *ca.* 0.5–1.5 μ, yellowish brown to chestnut; with cylindrical warts 0.2–1.0 μ high, 0.2–0.4 μ wide, 0.4–1.5 (1.8) μ spacing;

usually 1–4 distinct internal swellings (Fig. 3). This species has also been seen on: *Carex chordorrhiza* (B.C., Que.), *C.* ? *diandra* (Wyo.), *C. lanuginosa* (Wyo.), *C. lasiocarpa* var. *americana* (Ont.), *C. rhynchophysa* (Yukon), *C. vesicaria* (Ont.).

CINTRACTIA ASPERA Liro (Mycoth. fenn. 41. 1934)

Liro (9, p. 18) published this smut as a new species, but the Mycotheca fennica specimen was issued in 1934 with a nearly identical diagnosis. The point is of some importance because Liro gave no Latin diagnosis. The last valid date for descriptions without a Latin diagnosis is 31 Dec. 1934; thus, if the 1938 publication had been the first description issued, it would have been a *nomen nudum*. On this basis the packet of Mycoth. fenn. 41 in the University of Helsinki is to be regarded as the type. The following description is based on the University of Toronto isotype: Teliospores 18.0–24.0 × 11.5–20.5 μ, generally rounded. Wall 1.0–3.5 μ, chestnut to blackish brown, with more or less cylindrical warts 0.1–0.4 μ high, 0.2 μ wide, 0.4–1.2 μ spacing; without internal swellings. Three collections from Alaska and single specimens from northern Alberta, Fort George, Que., and Sweden give the following composite description: Teliospores 16.0–25.5 × 10.5–21.5 μ, rounded to rarely slightly angular or pointed. Walls 0.8–4.0 (4.7) μ, chestnut to blackish brown; with warts 0.1–0.7 (0.9) μ high, 0.2–0.5 μ wide, 0.4–1.6 μ spacing; without internal swellings. There is considerable variation in the size of the warts, but their general form, cylindrical and usually higher than wide, is relatively constant. Other distinguishing characters, such as size, shape, great range of wall thickness, and lack of internal swellings, show little variation and define the species clearly. Hirschhorn (6) placed this species in *Cint. microsora*, which is quite distinct and is best regarded as a variety of *Cint. caricis*; but to accept such an inclusive species concept is to destroy all understanding of the group.

Carex chordorrhiza inhabits mud at the edges of shallow pools in the arctic and *Sphagnum* bogs south of tree line. Although the available specimens indicate that it takes *Cint. aspera* in the northern and *Cint. fischeri* in the southern parts of its range, the division is not by habitat, for the specimens of *Cint. aspera* from southern Alaska and northern Alberta are from bogs.

CINTRACTIA SUBINCLUSA (Koerner) Magnus (Verhandl. Bot. Ver. Prov. Brandenb. 37 : p. 79. 1895)

(*Ustilago subinclusa* Koerner, in Rabenhorst, Hedwigia 13 : p. 159. 1874).

No specimens have been seen from the type host, *Carex riparia* (sect. Paludosae), but material is available on *C. atherodes* in this section, and on various species in sects. Hirtae, Lupulinae, and, particularly, Vesicariae. Agreement between hosts is generally as close as between collections on a given host species. On most hosts maximum spore length is generally 22–23 μ, but in the one specimen on *Carex saxatilis* (Churchill, Man.) and in one of four on the closely related *C. miliaris* (Great Whale River, Que.) a few spores run up to 25 μ long. However, in the three remaining specimens (Great Whale

River and near Fort George, Que., and St. Anthony, Nfld.) the dimensions are typical and it does not seem feasible at present to recognize any distinction. The following description is based on 19 specimens on the hosts listed: Teliospores 13.0–23.0 (25.0) × 10.5–20.0 (21.0) μ, rounded. Wall *ca.* 0.5–1.5 μ (obscured by warts), light to dark brown; warts cylindric to irregular, truncate or spreading slightly at apex, pale, (0.3) 0.5–1.8 μ high, 0.3–1.6 μ wide (occasionally to 2.0 μ long), 0.7–3.0 μ spacing; no internal swellings (Fig. 2). On *Carex atherodes* (Sask.), *C. lupuliformis* (Wis.), *C. miliaris* (Que., Nfld.), *C. physocarpa* (Alaska), *C. retrorsa* (Ont.), *C. rostrata* (Wyo.), *C. saxatilis* (Man.), *C. vesicaria* (Ont.). F. Columb. 2615 and another Wisconsin specimen examined, both issued as on *Carex lupulina*, are actually on *C. lupuliformis*. Dr. H. C. Greene states the same to be true of one other specimen, but that others lack normal achenes by which they might be distinguished. It must be presumed that *C. lupulina* is not a recorded host.

Cintractia caricis-oederi Lehtola, on *Carex oederi* in Finland has not been seen. Lehtola's (7) description suggests that it may be a small-spored variant of *Cint. subinclusa*.

CINTRACTIA SCIRPI (Kühn) Schellenberg (Die Brandpilze der Schweiz. p. 77. 1911)
(*Ustilago scirpi* Kühn, Hedwigia 12 : p. 150. 1873).

Six North American collections, all on *Scirpus caespitosus* var. *callosus*, have been studied. All are from Quebec, but since three are from the Hudson Bay Coast, one from L. Mistassini, one from Fort Chimo on Ungava Bay, and one from the Gaspé Peninsula, a great area is involved. A composite description follows: Teliospores (16.0) 17.0–24.0 (25.0) × (11.0) 12.0–21.0 (23.0) μ, rounded or rarely slightly irregular. Wall 1.0–2.7 (3.0) μ, blackish brown, smooth to minutely roughened; without internal swellings. Kunze F. Sel. 19, on *S. caespitosus* in Europe falls well within the above range.

CINTRACTIA EXTERNA (Griff.) Clinton (J. Mycol. 8 : p. 142. 1902)
(*Tilletia externa* Griffiths, Bull. Torr. Bot. Club. 29 : p. 290. 1902).

The type collection of this species (Griff. W. Am. Fungi 305, Buffalo, Wyo.) has spores 16.0–22.0 × 13.5–19.5 μ, rounded. Wall 1.5–3.2 μ of which about half is a chestnut to blackish brown inner layer and half a hyaline outer layer, smooth, without internal swellings. Examination of 14 collections from Saskatchewan on *Carex filifolia* shows that early in the season the spores regularly have this gelatinous, hyaline outer coat, which may even make it necessary to moisten the sorus before preparing a mount; but that this outer sheath generally disappears as the season progresses, by shrinkage, weathering, or both. No doubt both the degree of its development and its persistence depend somewhat on weather conditions. This fact probably explains the assignment of some specimens on this sedge to *Cintractia caricis*, e.g. Fungi Columb. 4808, which is definitely *Cint. externa* without the outer sheath. *Carex filifolia*, used here to include several segregates recognized by some authorities, does also take *Cint. carpophila*, but all other specimens seen (Sask.,

N.D., Wyo., Colo.) are *Cint. externa*. A composite description follows: Teliospores 16.0–23.0 × (10.0) 11.5–20.0 μ, excluding the hyaline outer sheath, rounded. Wall 0.8–2.0 μ, chestnut to dark brown, smooth or rarely minutely roughened, often with a conspicuous hyaline outer sheath 0.5–2.0 (3.0) μ thick, especially early in the season; without internal swellings. The inconstancy of the outer sheath necessitates its exclusion from spore measurements, in order to avoid unreal size differences. It will be seen that, barring the hyaline sheath, there are only minor distinctions between this species and *Cint. scirpi*.

Cintractia atratae Savile sp. nov.

Sori fuliginosi, in ovariis. Teliosporae 15.0–24.0 × 11.0–21.0 μ, compressae, ellipsoideae, nunquam angulater. Episporium 0.7–1.8 μ crass. verrucis exclusis, castaneum; verrucae ab hemisphericis elongatae, frequenter picturam labyrinthiformem delineantes, 0.1–0.4 μ alt., 0.4–1.0 μ lat. (vel usque ad 2.5 μ long.), quorum centrum a centro abest 0.5–1.5 μ; gibbera interna desunt.

In ovaries of *Carex atrata* L.: Glacier National Park, Mont., 27 Aug. 1915, leg. E. T. Bartholomew, Fungi Columb. 4908, Mycological Herbarium, Division of Botany and Plant Pathology, Ottawa (TYPE); and Leadville, Colo., 1896 (collector unknown). Two specimens on the related *C. reynoldsii*, Medicine Bow Mts., Wyo., (W. G. Solheim 2006 and Solheim and C. L. Porter 1902), are indistinguishable, as are two on *C. podocarpa*, Medicine Bow Mts., Wyo., (J. F. Brenckle 41–314 and L. H. Shinners), and near Carcross, Yukon (J. M. Gillett 4582 and D. A. Mitchell). Fungi Columb. 2415 on *Carex* sp. (Wyo.) agrees well except that the warts are somewhat shallow; it was issued as on *Carex stricta*, an eastern plant, but it is impossible to determine the host from the material seen. A closely related smut has been seen on *Carex miliaris* and the related *C. saxatilis* var. *laxa* at Great Whale River, Que., and on *C. miliaris* near St. Anthony, Nfld. Further study may warrant its segregation as a variety.

CINTRACTIA CARICIS (Pers.) Magnus (Verhandl. Bot. Ver. Prov. Brandenb. 37 : p. 79. 1895) var. CARICIS

(*Uredo caricis Persoon, Synopsis Meth. Fung., p. 225. 1801*).

(*Cintractia caricis* (Pers.) Magn. var. *eructans* Kunze, F. Sel. 208. 1880).

(*Cintractia eructans* (Kunze) Liro (9) p. 33. 1938).

(*Cintractia turfosa* Sydow (12) p. 289. 1924).

There has never been any clear or general understanding of this taxonomically fundamental species. Clinton (3) and Sydow (12) gave *Carex montana* as the type host, but Liro (9, p. 236) has shown that Persoon's plant must have been *C. pilulifera*. The desirability of accepting *C. pilulifera* as the type host is enhanced by the fact that this sedge harbors a single, well-known smut of which abundant specimens are available. Specimens on *C. montana* are scarce and it is possible that two smuts occur on it; for, although Sydow

describes the spores as 14–18 × 13–16 μ, Sydow Ustil. 264 (Univ. of Toronto), the only specimen available, has spores 17–25 × 11.5–21 μ, which indeed agree well with those of the fungus on *C. pilulifera*. The description below, based on Liro Mycoth. fenn. 32 and two other Scandinavian specimens on *C. pilulifera*, will serve to define *Cint. caricis* as it is here understood. Lehtola's (7) tabulation of 17 collections gives a total range of 15–27 × 11–21 μ for spore sizes, very close to those in the following description: Teliospores (16.0) 17.0–25.0 (26.5) × 10.5–20.5 (22.0) μ, usually strongly angular or externally lobed or ridged. Wall 1.0–2.5 μ, or to 3.2 μ at angles, blackish brown; warts rounded, 0.1–0.4 (0.5) μ high, 0.2–0.4 μ wide (rarely slightly elongate), 0.5–1.7 μ spacing, without internal swellings (Fig. 6). Sydow Ustil. 75 and Liro Mycoth. fenn. 31 on *Carex dioica*, both supposedly *Cint. turfosa*, are not safely distinguishable. The same is true of Kunze F. sel. 208 on *Carex hirta*, the type of *Cint. eructans*. It should be noted, however, that the packet seen of Allescher & Schnabl F. bavar. 501 is a different smut more closely allied to *Cint. irregularis* Liro.

North American specimens seen that agree closely are on: *Carex artitecta* (Ont.), *C. aurea* (Que.), *C. capillaris* (Keew., Que., Nfld.) *C. livida* (Alaska, N.D.), *C. multicaulis* (Calif.), *C. pensylvanica* var. *distans* (Que.), *C. pensylvanica* var. *pensylvanica* (Que.), *C. rupestris* (Keew., Man., Frank., Que., Nfld., Greenl.), *C. supina* (Que.), *C. tetanica* (N.D.), *C. umbellata* (Que.).

On several hosts or groups of hosts there is considerable range of intergrading forms related to *Cintractia caricis*, although the degree of variation in any one collection is relatively small. Study of the whole complex makes it desirable to recognize two new varieties at least. It is possible that others may have to be added later. A form having somewhat less angular spores than the typical variety, with occasional, shallow internal swellings, is designated:

CINTRACTIA CARICIS (Pers.) Magn. var. **intermedia** Savile var. nov.

Teliosporae (14.0) 15.0–24.0 (25.0) × 9.0–19.0 (21.0) μ, rotundatae vel angulatae. Episporium 0.5–2.0 (2.5) μ, castaneum; verrucis 0.1–0.2 (0.3) μ alt., 0.2–0.4 μ lat., quorum centrum a centro abest 0.3–1.6 μ; interdum interne gibberibus 1–2 paullum eminentibus munitum.

In ovaries of *Carex pensylvanica* Lam. var. *pensylvanica* Victoria Beach, Man., 22 June 1935, leg. I. L. Conners (DAOM 2653) (TYPE). Nine other collections on this host from Saskatchewan, North Dakota, Manitoba, Wisconsin, and southern Ontario agree closely with the type, but others from eastern Ontario, western Quebec, Massachusetts, New Hampshire, and New York approach var. *caricis*. As already indicated, one Quebec collection (Richelieu Co.) is typical of var. *caricis*. There is, on this host, a suggestion of a geographic cline, but no clear indication of one can be seen when the other hosts of this complex are considered. North American specimens referable to var. *intermedia* occur on: *Carex abdita* (N.S.), *C. capillaris* (Man.), *C. deflexa* (Mack., Greenl.), *C. geyeri* (Wyo.), *C. glacialis* (Que.), *C. gmelini* (Alaska), *C.*

lyngbyei ssp. *cryptocarpa* (Alaska), *C. norvegica* (Que.), *C. obtusata* (Yukon), *C. supina* (Mack.). This variety seems to be less common in Europe than in North America.

The trend toward lessened angularity and increase of internal lobing is followed further in the next variety, which is perhaps the most primitive of the three.

CINTRACTIA CARICIS (Pers.) Magn. var. **acutarum** Savile var. nov.

Teliosporae 14.0–27.5 × 9.5–21.0 μ, rotundatae vel raro leviter angulatae. Episporium 0.8–3.2 μ crass.; verrucis rotundatis 0.1–0.3 μ alt., 0.1–0.4 μ lat., quorum centrum a centro abest 0.5–1.5 μ; saepius interne gibberibus 1–3 paullum eminentibus munitum.

In ovaries of *Carex aquatilis* Wahl.: South Intake, 40 mi. E. of Dawson, Yukon, 20 Aug. 1949, leg. J. A. Calder 4588 and L. G. Billard (TYPE); common on this host from coast to coast (Alaska, Yukon, B.C., Mack., Alta., Ida., Sask., Keew., Man., Ont., Que., Nfld.)), and *C. sitchensis* (B.C., ? Wash.), also in sect. Acutae, subsect. Vulgares, and on *C. haydenii* (Que.) in subsect. Strictae. The following records on hosts in the related sect. Cryptocarpae are of an indistinguishable and perhaps biologically identical fungus: *Carex lyngbyei* ssp. *cryptocarpa* (Alaska), *C. paleacea* (Que.), *C. ramenskii* (Alaska), *C. salina* var. *kattegatensis* (Que.), *C. salina* var. *salina* (Labr., Nfld.). Referable here, although probably in part, at least, physiologically distinct are specimens on: *Carex deweyana* (Ont.), *C. livida* (Alaska, Que., Nfld.), *C. supina* (Sask.). Further material on *Carex livida* is needed. Some specimens fit well in the present variety or var. *caricis*, but others show appreciable differences and may belong to a distinct species.

Cintractia variabilis Lehtola (7, p. 45) was described from the composite measurements of 130 collections, mostly Finnish, on *Carex nigra* (*C. goodenowii*). No type was designated and it cannot be stated definitely that only one fungus is involved. It may be noted that *C. nigra* takes at least two other *Cintractia* spp. in Europe. From the description *Cint. variabilis* appears to be close to but distinct from *Cint. caricis* var. *acutarum*. A single Swedish specimen seen on this host, with moderately angular spores that lack internal swellings, is scarcely distinguishable from *Cint. caricis* var. *caricis*; but it is not certain whether it is Lehtola's organism.

Sydow Ustil. 223, on *Carex remota* in Japan, was issued as *Cint. caricis* and later made the type of *Cint. microsora*, largely on the basis of the small sori. It appears to be referable here.

CINTRACTIA LIMOSA Sydow (12, p. 228. 1924) var. LIMOSA

The following description is based on 13 collections on *Carex limosa* from Canada (Alta., Sask., Man., Ont., Que., Labr., Nfld.) and five from Europe, including Sydow Ustil. 76, 77, and Sydow Myc. germ. 219. Teliospores (17.5) 19.0–30.0 × 13.0–25.5 μ, rounded or rarely slightly angular. Walls (0.8) 1.0–2.7 (3.0) μ, blackish brown; warts 0.1–0.4 μ high, 0.2–0.6 μ wide, 0.5–2.0 μ spacing; without internal swellings (Fig. 4). Field observations

indicate that this and the next variety, or at least a race of each, infect both *Carex limosa* and the closely related *C. rariflora*, but that *C. paupercula* takes different races. Specimens on *C. rariflora* from Keewatin and Newfoundland belong to this variety as do four from Alaska on *C. paupercula*, which is also in sect. Limosae. Morphologically similar, though perhaps physiologically distinct, smuts have been seen on the following species in other sections: *Carex bigelowii* (Que.), *C. buxbaumii* (Alaska, Que.), *C. gynocrates* (Que.), *C. lasiocarpa* var. *americana* (Alaska), *C. nigricans* (Calif.), *C. salina* var. *salina* (Labr.), *C. salina* var. *subspathacea* (Keew.), *C. scirpoidea* (Yukon, Alta., Man., Nfld.), *C. vaginata* (Yukon, Mack., Alta., Man., Que., Nfld.). The spores from *Carex vaginata* show slightly more angularity than is typical and vary slightly from specimen to specimen. The Newfoundland specimens tend to have somewhat small spores; and in single specimens from Yukon and Mackenzie, but not in others, there is a suggestion of internal lobing.

CINTRACTIA LIMOSA Sydow var. **gigantissima** (Lehtola) Savile comb. nov.
(*Cintractia gigantissima* Lehtola (7, p. 129. 1940)

Teliospores 22.0–33.0 (35.0) × (14.0) 15.5–28.0 (30.0)μ. Wall 1.0–2.8 (3.5)μ thick. Otherwise indistinguishable from var. *limosa*. *Cint. gigantissima* was erected on the basis of five specimens on *Carex rariflora* that seemed to have spores uniformly larger than those of *Cint. limosa*; but Canadian collections on both *Carex limosa* and *C. rariflora* show all intergradations. Twenty-five collections, more than half from Alaska, on hosts in sect. Limosae are referable to this variety: *Carex limosa* (Alaska, Man., Nfld.), *C. rariflora* (Ont., Que., Nfld.), × *C. firmior* (*limosa* × *rariflora*) (Nfld.), *C. paupercula* (Alaska), *C. pluriflora* (Alaska). A single specimen on *C. montanensis* (sect. Atratae) from Yukon Territory is also referred to this variety. The assignment of some intermediate specimens must be arbitrary and the maintenance of *Cint. gigantissima* as a species seems to be out of the question. It seems necessary to maintain both it and the next taxon as varieties, however, for no single specimen even approaches the size range of the series.

A single sorus on *Carex lyngbyei* ssp. *cryptoparpa* from Alaska is provisionally placed here, although the shape of both spores and warts is not quite typical.

CINTRACTIA LIMOSA Sydow var. **minor** Savile var. nov.

Teliosporae 17.0–23.5 (25.5) × 12.0–22.0 (24.0) μ, rotundatae, compressae, ellipsoideae. Episporium 1.0–2.2 μ crass., atrobrunneum; verrucis 0.1–0.4 μ alt., 0.2–0.5 μ lat., quorum centrum a centro abest 0.8–1.5 μ; gibbera interna desunt.

In ovaries of *Carex bigelowii* Torr.: Great Whale River, Que., 28 July 1949, leg. D.B.O. Savile 536 (TYPE). Five other collections on *C. bigelowii* from Great Whale River, Fort George and near Fort Chimo, Que., and Bathurst Inlet, Mack., belong to this variety, but another from Fort George is assignable to var. *limosa*. One specimen from Fort George on *C. paupercula* fits this variety. Ten collections on *C. scirpoidea* (Alaska, Alta., Wyo., Que., Nfld.) fit better in this variety than in var. *limosa* to which five others are assigned,

but there is some intergradation. The majority of specimens are clearly distinct from the two larger-spored varieties, but it does not appear feasible to erect a separate species. Smuts on the following sedges may be placed in var. *minor* although some show small distinctions: *Carex atrofusca* (Keew., Greenl.), *C. douglasii* (Ore., Nev., Colo.), *C. foenea* (Mack., Alta., Wyo., Colo., Ont.), *C. lugens* (Yukon), *C. misandra* (Keew.). Single fragmentary specimens from Idaho and Wyoming on *C.* ? *gymnoclada*, or some other species close to *C. bigelowii*, evidently belong here also. Some collections on *C. vaginata* approach this variety. The specimens on *C. foenea* and *C. lugens* have spore walls up to 3.0 μ thick. There seem to be several species originating from this complex, but they cannot yet be safely distinguished. It should be noted that the smut on *Carex douglasii* was called *Ustilago caricis* var. *douglasii* by Shear (Fungi Columb. 1485) and *Cintractia caricis-douglasii* by Ciferri (2, p. 44). Since neither name was validated by a description they are best abandoned.

CINTRACTIA CALDERI Savile (Can. J. Bot. 29 : p. 324. 1951)

Teliospores 21.0–32.0 × 19.0–24.0 (26.0) μ, flattened ellipsoidal, never angular. Wall *ca.* 1.0–1.5 μ, opaque black; warts dark brown, subcylindric, rounded above, *ca.* 0.5–1.5 μ high, 0.5–1.5 μ wide (occasionally to 2.5 μ long by fusion), 0.9–3.0 μ spacing; apparently without internal swellings (Fig. 5). Heavy pigmentation makes wall thickness and height of warts difficult to determine.

In ovaries of *Carex backii*: Gillam, Man., and Port Hope, Ont. Sori largely concealed by sheathing bracts of the inflorescence. Specimens of *Carex backii* and *C. saximontana* should be scrutinized for this smut. *Cint. calderi* is apparently related to *Cint. limosa* from which it is readily distinguished by the large warts on the spore walls.

CINTRACTIA PRATENSIS Sydow (12, p. 289. 1924)

This species was described from *Carex diversicolor* (*C. glauca*), Sydow Ustil. 6, 122, and 389 being cited as examples. The following description is based on five specimens, all in close agreement, upon this sedge, including Sydow Ustil. 6 and 122, and Fl. Hung. Exs. 501; the latter was issued as being on *Carex clavaeformis*, but Liro (9, p. 241) points out that the host is *C. diversicolor*. Teliospores 19.0–28.0 (30.0) × 12.5–23.5 μ, rounded to moderately angular or irregular. Wall 1.0–3.5 (4.5) μ thick, blackish brown to black; warts 0.1–0.3 μ high, 0.1–0.3 μ wide, 0.5–2.0 μ spacing; often 1–2(3) small internal swellings.

The only new world collections seen that are referable to this species are one on *Carex exilis* from Fort George, Que., and one on *C. holostoma* from Chesterfield Inlet, Keew. Except for its internal swellings, *Cint. pratensis* seems to be intermediate between *Cint. limosa* and the old-world complex of *Cint. irregularis* and related forms with large, extremely angular spores. Further study may indicate the need of reducing *Cint. pratensis* to a variety of one of the latter group, but it seems advisable to maintain it for the present.

Excluded Species

Cintractia arctica (Rostrup) Lagerheim (in Blytt, Forhandlinger Videnskabs-Selskabet Christiania, 6 : p. 30. 1896)
(*Tilletia arctica* Rostrup, Bot. Tidskrift, 15 : p. 230. 1886.)

This curious fungus is known to attack species of *Carex* of sect. Heleonastes in northern Scandinavia and of sect. Ovales, subsect. Festivae in Scandinavia and North America. The only American specimen known to the writer is one taken by Fischer, Sprague, and Meiners at Grand Mesa, Colo., 6 Aug. 1948, on *Carex ebenea*. The only other specimen seen is Rab.-Pazs. F. europ. 4101, on *Carex glareosa*, on the basis of which Lagerheim placed the fungus in *Cintractia*. There are small differences between the spores of these two collections, but they may be only chance variations. Certainly the two fungi are essentially similar. It is equally clear that there seems to be no justification for placing them in *Cintractia*. Dr. Fischer lent the writer the whole of his collection and from it the bahavior of the fungus was worked out to some extent. The fungus is evidently systemic and perennial in the base of the host. Infected plants are sterile and otherwise abnormal. It is believed that the fungus fruits between the leaf bases in the meristematic zone, forming crusts of spores that are carried upward and exposed by the elongation of the leaves, a mechanism that could only operate with monocotyledonous plants. This smut, if such it is, is described as producing linear sori on the leaves, which suggests a similarity to *Schizonella*; but the mature spores have no protoplasmic connection with the leaf, which has an intact epidermis and contains no mycelium in the upper parts. This fungus probably is a smut, but the spores have apparently never been germinated and little is known of its biology. Rostrup described this fungus from *Carex macloviana* and it is, therefore, reasonable to suppose that the Colorado specimen is identical with it in view of the close relationship of the hosts. The spores of the Colorado specimen are 13.0–19.0 (20.0) × 11.0–15.0 μ, rounded. Wall *ca.* 0.9–1.2 μ, yellow-brown to light chestnut; with large shallow, rounded, often elongate depressions, *ca.* 0.3–0.5 (0.8) μ deep, (0.3) 0.5–1.5 μ wide or to 2.0 μ long or rarely confluent, 1.0–1.8 μ spacing, discounting elongate depressions; without internal swellings. The wall depressions are closely spaced, leaving a network of ridges only about 0.2 μ wide at the top.

The writer believes that this organism is a smut, but is unwilling to assign it to a genus until it is better understood. In the meantime attempts should be made to work out its life history. Germination of the spores may prove difficult, but it may be possible to culture the fungus from the meristematic tissue at the base of infected plants. Mycologists in the Rocky Mountains region are urged to be on the watch for infected colonies of *Carices* in subsect. Festivae and to secure living material.

TABLE I

HOST DISTRIBUTION OF *Cintractia* SPP. ON *Carex*, *Kobresia*, AND *Scirpus*

Cintractia spp.	*carpophila carpophila*	*carpophila elymae*	*carpophila kenaica*	*carpophila verrucosa*	*fischeri*	*subinclusa*	*aspera*	*externa*	*scirpi*	*caricis caricis*	*caricis intermedia*	*caricis acutarum*	*atratae*	*limosa minor*	*limosa limosa*	*limosa gigantissima*	*pratensis*	*calderi*
Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Scirpus caespitosus									X									
Kobresia																		
myosuroides	x[1]	X[2]																
K. simpliciuscula		X																
Carex spp.																		
NARDINAE																		
nardina	X																	
CALLISTACHYS																		
nigricans															X			
pyrenaica ssp.																		
micropoda			X															
DIVISAE																		
douglasii														X				
praegracilis	X[2]	X																
ARENARIAE																		
foenea														X				
CHORDORRHIZAE																		
chordorrhiza					X		X											
PANICULATAE																		
? diandra					X													
HELEONASTES																		
disperma	X																	
trisperma	X																	
tenuiflora ×																		
? gynocrates	X																	
loliacea	X																	
lachenalii		X																
marina	x	X																
glareosa	x																	
brunnescens	X																	
canescens	X				X													
DIOICAE																		
gynocrates	X														X			
STELLULATAE																		
exilis																	X	
interior	X																	
angustior	X																	

[1] x *Indicates specimens that are not quite typical.*

[2] X *Indicates typical specimens.*

[3] *Host identity doubtful.*

TABLE I—*Continued*

HOST DISTRIBUTION OF *Cintractia* SPP. ON *Carex*, *Kobresia*, AND *Scirpus*—*Continued*

Cintractia spp.	*carpophila carpophila*	*carpophila elynae*	*carpophila kenaica*	*carpophila verrucosa*	*fischeri*	*subinclusa*	*aspera*	*externa*	*scirpi*	*caricis caricis*	*caricis intermedia*	*caricis acularum*	*atratae*	*limosa minor*	*limosa limosa*	*limosa gigantissima*	*pratensis*	*calderi*
Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
DEWEYANAE																		
bromoides	X																	
deweyana			X									X						
OVALES																		
Festivae																		
? festivella				X														
ebenea				X														
macloviana ssp. *pachystachya*				X														
Leporinae																		
praticola	X																	
Foeneae[4]																		
aenea	X																	
PHYLLOSTACHEAE																		
backii																		X
FILIFOLIAE																		
filifolia	X							X										
OBTUSATAE																		
obtusata											X							
supina										X	X	X						
MONTANAE																		
artilecta										X								
pensylvanica																		
var. *p.*										X	X							
pensylvanica var. *distans*										X								
deflexa											X							
rossii	X										X							
abdita											X							
umbellata										X								
SCIRPINAE																		
scirpoidea														X	X			
RUPESTRES																		
rupestris										X								
glacialis											X							

[4] *Subsection based on Carex argyrantha (C. foenea Auth., not Willd.).*

TABLE I—*Continued*

HOST DISTRIBUTION OF *Cintractia* SPP. ON *Carex*, *Kobresia*, AND *Scirpus*—*Continued*

Cintractia spp.	*carpophila carpophila*	*carpophila elynae*	*carpophila kenaica*	*carpophila verrucosa*	*fischeri*	*subinclusa*	*aspera*	*externa*	*scirpi*	*caricis caricis*	*caricis intermedia*	*caricis acutarum*	*atralae*	*limosa minor*	*limosa limosa*	*limosa gigantissima*	*pratensis*	*calderi*
Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
FIRMICULMES																		
multicaulis										X								
geyeri											X							
ALBAE																		
eburnea										x								
BICOLORES																		
aurea										X								
PANICEAE																		
livida										X		X						
tetanica										X								
vaginata															x			
LAXIFLORAE																		
leptonervia	X																	
CAPILLARES																		
capillaris										X	X							
FERRUGINEAE																		
petricosa	X																	
misandra														X				
atrofusca														X				
HIRTAE																		
lanuginosa	X				X	X												
lasiocarpa var. *americana*					X										X			
LIMOSAE																		
rariflora															X	X		
limosa															X	X		
firmior																X		
pluriflora																X		
paupercula														X	X	X		
ATRATAE																		
norvegica											X							
holostoma																	X	
montanensis																X		
gmelini											X							
buxbaumii												X[5]			X			
podocarpa													X					
reynoldsii													X					
atrata													X					

[5] *Probably not a normal host for this smut; see text.*

TABLE I—*Concluded*

HOST DISTRIBUTION OF *Cintractia* SPP. ON *Carex*, *Kobresia*, AND *Scirpus*—*Concluded*

Cintractia spp.	*carpophila carpophila*	*carpophila elynae*	*carpophila kenaica*	*carpophila verrucosa*	*fischeri*	*subinclusa*	*aspera*	*externa*	*scirpi*	*caricis caricis*	*caricis intermedia*	*caricis acutarum*	*atratae*	*limosa minor*	*limosa limosa*	*limosa gigantissima*	*pratensis*	*calderi*
Host	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
ACUTAE																		
Rigidae																		
bigelowii														X				
? *gymnoclada*														X				
Vulgares																		
nigra												X						
sitchensis												X						
aquatilis												X						
Sentae																		
lugens	X														X			
Strictae																		
haydenii												X						
stricta	X																	
CRYPTOCARPAE																		
paleacea												X						
lyngbyei ssp.																		
cryptocarpa											X	X				x		
ramenskii												X						
salina var.																		
salina												X			X			
salina var.																		
subspathacea															X			
salina var.																		
kattegatensis	X											X						
ORTHOCERATES																		
pauciflora	X																	
PALUDOSAE																		
atherodes	X					X												
VESICARIAE																		
miliaris						X							x					
saxatilis						X							x					
physocarpa						X												
vesicaria					X	X												
rostrata					X	X												
rhynchophysa					X													
retrorsa						X												
LUPULINAE																		
lupuliformis						X												

Phylogeny

Table I has been prepared to bring together the taxonomic data, of which some significant details are likely to be otherwise overlooked.

The species of *Carex* are, with few exceptions, listed in the sequence of Mackenzie (10) and under his sections and subsections. The groupings are probably fairly natural, but the sequence of the sections is open to argument, since a linear arrangement can never be wholly satisfactory.

It is clear that the different varieties of *Cintractia carpophila* occur most abundantly on the earliest sections, especially up to and including Ovales, which marks the end of the subgenus *Vignea*. However, this species occurs sparingly in various other sections. Several other correlations are evident, notably: the predominance of *Cint. caricis* var. *caricis* and var. *intermedia* in sect. Montanae and to some extent in neighboring sections; of *Cint. limosa* vars. in sect. Limosae; of *Cint. caricis* var. *acutarum* in sect. Acutae subsect. Vulgares and in sect. Cryptocarpae; and of *Cint. fischeri* and *Cint. subinclusa* in sect. Vesicariae.

A few less conspicuous associations may also be indicated. Within sect. Heleonastes the three closely related species *Carex lachenalii*, *C. marina*, and *C. glareosa* take *Cint. carpophila* var. *elynae* or an intermediate form, whereas the remaining species take typical *Cint. carpophila* var. *carpophila*. It is of interest that agreement is particularly close between the smuts on *Carex gynocrates* in the next section and *C. disperma*, *C. trisperma*, and the *C. tenuiflora* hybrid of which *C. gynocrates* is the presumptive second parent.

Subsections tend to be set up as a matter of convenience in sections that contain many species, although it is possible that equally great distinctions may sometimes occur within smaller sections. The segregations within sect. Ovales are supported by the limited smut records within the section, and those within sect. Acutae receive considerable support. It is interesting that subsect. Vulgares seems to show closer affinities with sect. Cryptocarpae than with the other subsections of its section.

Within sect. Vesicariae the smut records tend to support the quite evident separation of the hosts into a "saxatilis" group, represented by the first three species, and a "vesicaria" group.

The distribution of the *Cintractia carpophila* records suggests that this is a basic species of the group—*the* basic species if we can be certain that the group is monophyletic. If we make this assumption tentatively we may look upon rounded spores, small spore size, smooth walls, and possibly internal swellings as being primitive characters; but there is some doubt about the last, which seems to have recurred several times in the evolution of the group. We may then suppose that evolution has progressed in the direction of increasing angularity and size of spores, increasing roughness of walls and possibly decrease of internal swellings. According to these assumptions we may tentatively place *Cint. carpophila* var. *carpophila* at the base of the sequence, with the other three varieties derived from it. *Cint. fischeri*, *Cint. subinclusa*, and *Cint. aspera* may represent one evolutionary group from the "carpophila"

complex. The smooth-walled species of moderate size, *Cint. externa* and *Cint. scirpi*, may have been derived independently from the same complex, and from them *Cint. atratae* and the *Cint. caricis* group, starting with *Cint. caricis* var. *acutarum*. The *Cint. limosa* series, starting with var. *minor*, which shows affinity with both *Cint. atratae* and *Cint. caricis* var. *acutarum*, appears to have branched off from the same stock. From *Cint. limosa* or some form close to it two lines seem to have arisen, one giving rise to *Cint. calderi* and the other to *Cint. pratensis* and the old-world *Cint. irregularis* complex.

This hypothesis of two simultaneous lines of evolution seems to receive some support from the table. It will be seen that sects. Chordorrhizae, Paniculatae, Heleonastes, Hirtae, Paludosae, Vesicariae and Lupulinae contain all the records for *Cint. fischeri*, *Cint. subinclusa*, and *Cint. aspera*, but very few of those for the species to the right of them in the table. On the other hand the Eucarex sections (from sect. Phyllostachyae onward) other than Hirtae, Paludosae, Vesicariae, and Lupulinae contain most of the records for *Cint. caricis*, *Cint. atratae*, and the large-spored species.

It must be remembered that the data in the table are far from complete and may be misleading in some respects. On the other hand further data will probably explain some apparent anomalies by adding to the number of sedges that are known to take more than one smut. It is certainly true that the 150 or more specimens checked in recent months, since the first provisional scheme was drawn up, have greatly clarified the picture. It is not likely that further data will seriously upset it.

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References

1. Ainsworth, G. C. *Review of* The smut fungi *by* George William Fischer. Trans. Brit. Mycol. Soc. 34 : 607. 1951.
2. Ciferri, R. Quinta contribuzione allo studio degli Ustilaginales. Ann. Mycol. 29 : 1–74. 1931.
3. Clinton, G. P. North Am. Flora, 7 : Part 1. 1906.
4. Fernald, M. L. Gray's manual of botany. 8th ed. American Book Co. New York. 1950.
5. Hagen, A. Ustilagineae from East Greenland. Sydowia, 1 : 283–288. 1947.
6. Hirschhorn, E. Critical observations on the Ustilaginaceae. Farlowia, 3 : 73–93. 1947.
7. Lehtola, V. B. Untersuchungen über einige Brandpilze der gattung *Cintractia* Cornu. Suom. Maataloust. Seur. Julk. No. 42 : Part 1. 1940.
8. Linder, D. H. Fungi. *In* Botany of the Canadian Eastern Arctic *by* N. Polunin. Nat. Museum Can. Bull. 97. 1947.
9. Liro, J. I. Die Ustilagineen Finnlands. II. Ann. Acad. Sci. Fenn. Ser. A, 42. 1938.
10. Mackenzie, K. K. North Am. Flora, 18 : Parts 1–7. 1931–1935.
11. Savile, D. B. O. North American species of *Chrysomyxa*. Can. J. Research, C, 28 : 318–330. 1950.
12. Sydow, H. Notizen über Ustilagineen. Ann. Mycol. 22 : 277–291. 1924.
13. Zundel, G. L. I. North Am. Flora, 7 : Part 14. 1939.

LES ZONES BIOLOGIQUES DE LA PÉNINSULE QUÉBEC–LABRADOR ET L'HÉMIARCTIQUE[1]

PAR JACQUES ROUSSEAU[2]

Abstract

In order to place phytogeographical regions on a world basis, it is necessary to invoke the zone concept. For example, a botanist who studies the flora of some parts of the USSR, Alaska, Quebec, and Scandinavia recognizes many similarities, if not analogous floras: before considering the local differentiations which distinguish regional floras, he recognizes on first sight the "arctic" aspect. The tendency of phytogeographers, foresters, and biologists in general is to overlook the zonal division of the world from the arctic zone to the tropical zone and consider the regional aspects only. In a zonal division of Quebec, there are the *temperate zone*, grossly south of the 50° lat. N.; the subarctic zone, between the 50° and the 55° approximately; the *hemiarctic zone*, between the 55° and the absolute limit of trees; and finally the *arctic zone*, north of the 58°. The *hemiarctic zone*, described herein, and consisting principally of the habitat commonly called forest–tundra, is not formed of transitional habitats between those of the subarctic zone and those of the arctic zone, but made up of purely arctic patches (from 60 to 90% of the surface) imprisoned in a net of subarctic forest strips. The hemiarctic zone instead of being merely a mixture of arctic and subarctic plants, may be compared then to an "emulsion" of arctic and subarctic habitats. This "mixed" zone, highly convenient for phytogeographical purposes, finds its justification in biological and climatological data. For the distinction of the zones, we must not consider only the arborescent flora but all other expressions of life as well. From tentative studies, it is quite evident that a distinction of the zones based on limited floristic aspects,—the aquatic flora for example,—will lead to the same conclusion.

Introduction

La province de Québec et le Labrador sont les régions du globe où la zone arctique,—comprise au point de vue climatique et biologique,—atteint sa plus grande extension méridionale. Sous la même latitude que Stockholm, l'est du Canada est couvert par la toundra. Dès le 50° et le 51° de latitude nord, la forêt québécoise est subarctique. La faible élévation du pays élimine le passage brusque d'une zone climatique à l'autre. Ce qui, dans le nord de l'Europe, est quelque peu télescopé, se déploie sur une douzaine de degrés de latitude dans la péninsule Québec–Labrador.[3] C'est dire que cette région est particulièrement apte à l'étude de l'évolution spatiale de la couverture végétale depuis la zone arctique proprement dite jusqu'à la zone tempérée.

Deux études d'ensemble ont paru jusqu'ici sur les divisions phytogéographiques du Québec, celles du F. Marie-Victorin (65), en 1935, et de Marcel

[1] *Manuscrit original reçu le 9 juillet 1951, et, sous forme revisée, le 17 mars 1952. Contribution du Jardin botanique de Montréal, Montréal, Qué.*

[2] *L'auteur tient à remercier particulièrement tous ceux qui ont apporté leur collaboration au cours du travail, notamment M. Marcel Raymond, M. Ilmari Hustich, M. François Grignon, Mlle Simone Constant, Mlle Jacqueline Blain, Mme Béatrice Bergeron, et surtout l'Arctic Institute of North America, le National Defence Research Board, la Cité de Montréal (dont relève le Jardin botanique), le premier ministre et le Gouvernement de la province de Québec, qui, en favorisant mes travaux d'exploration dans le nord de la péninsule Québec–Labrador, m'ont permis de mettre ce travail sur le métier.*

[3] *Le nom Labrador, fréquemment étendu à tort à l'ensemble de la péninsule Québec–Labrador, doit être restreint à la zone littorale appartenant à Terre-Neuve. La partie du Québec au nord du 52° lat. N., grosso modo, porte le nom de Nouveau–Québec ou Ungava. L'ensemble de la péninsule n'ayant pas de nom approprié, j'ai proposé en 1949 celui de péninsule Québec–Labrador (105).*

Raymond (85), en 1950 (rédigée toutefois dès 1947). Aussi, dans l'étude de Marcel Raymond comme dans celle du F. Marie-Victorin on n'a pu tenir compte des résultats acquis ces dernières années, au cours des premières explorations botaniques de l'intérieur de l'Ungava effectuées par l'abbé Ernest Lepage, le père Arthème Dutilly et Jacques Rousseau. Il importe également de mentionner ici une autre étude intéressant les travaux de phytogéographie, l' "Aperçu climatique du Québec" de Villeneuve (130).

Le présent travail ne prétend pas résumer la phytogéographie québécoise, mais cherche à situer dans son cadre une zone biologique nouvelle que l'exploration de l'Ungava a permis de délimiter, la *zone hémiarctique.* Les données du travail reposent surtout sur l'exploration des rivières George, Kogaluk, Payne, Korok et Adloylik et des monts Otish, poursuivie en 1947, 1948, 1949, 1951 par l'auteur (105).

Les zones climatiques et biologiques

La terminologie phytogéographique est trop souvent inadéquate. En définissant des régions particulières, il importerait de les situer sur le plan mondial. C'est là qu'intervient le concept de zone. La zone est un élément géographique latitudinal, plus ou moins large suivant les pays, mais identifiable au moyen d'éléments communs ou analogues. Le botaniste qui parcourt les territoires russes, alaskiens, islandais, groenlandais ou canadiens au nord de la limite des arbres, reconnaît les similitudes. Il identifie ainsi la zone arctique. Poussant l'étude plus avant, il reconnaîtra que le territoire arctique de l'extrémité boréale du Québec n'est pas absolument semblable à la partie arctique de l'Alaska, ni à l'Islande. De là la distinction de régions.

Pour Merriam (69, 70), le nord de l'Amérique se divise en un grand nombre de régions distinctes, basées surtout sur des caractéristiques faunistiques. Leur répartition sur un plan mondial est des plus confuses, ce qui a permis aux auteurs subséquents d'interpréter sa classification de façons extrêmement variées. Rares sont les botanistes attribuant à Merriam ce qu'il a réellement écrit, précisément parce qu'ils le connaissent à travers d'autres ouvrages déformant sa pensée. Le premier travail de Merriam est extrêmement confus, ce qui ne l'empêche pas de renfermer une documentation précieuse.

L'une des meilleures et plus récentes applications des principes de Merriam se trouve dans Dice (16). Ses provinces biotiques sont des régions distinctes que l'auteur ne rattache généralement pas aux grandes zones climatiques. Ainsi, les différentes provinces biotiques soumises à un régime de climat tempéré semblent, dans sa classification, aussi distinctes l'une de l'autre (même s'il y a de grandes similitudes) que ne le sont par exemple une province biotique du Texas et celle de l'archipel arctique. Ses provinces biotiques du Canada, réduites à la plus simple expression (et moins subdivisées que les provinces des Etats-Unis), correspondent pratiquement aux zones climatiques. Ainsi, si l'on ne considère que la péninsule Québec–Labrador et le territoire avoisinant, la province biotique esquimaude (eskimoan province) comprend grosso modo tout le Québec arctique; la province biotique hudsonienne

(hudsonian) englobe la zone subarctique et celle que je nomme hémiarctique, et la province biotique canadienne (canadian) comprend approximativement le Québec tempéré.

Pour Harshberger (37), Marie-Victorin (65), et la plupart des botanistes américains, il existe une vaste zone boréale couvrant l'hémisphère nord, depuis le pôle jusqu'à la zone tropicale. Leur zone boréale se divise ensuite en vastes régions (basées sur des caractères floristiques, mais inspirés de Merriam), dont la région hudsonienne. Celle-ci a forcément son pendant dans le nord de l'Europe, mais rien dans la terminologie de Merriam et de ses disciples ne l'indique. Il serait plus pratique, à la vérité, de distinguer d'abord des zones qui ne soient pas un hémisphère presque entier. Suivant les divisions géographiques classiques, nous avons du pôle nord à l'équateur, les zones arctique, subarctique, tempérée, subtropicale et tropicale. Je propose en outre d'intercaler la zone hémiarctique entre l'arctique et la subarctique. La région hudsonienne telle que définie par Merriam, et s'étendant sur dix degrés de latitude dans le Québec, couvrirait donc deux zones différentes, l'hémiarctique et la subarctique.

Macoun et Malte (62) ont partagé botaniquement le Canada en 11 divisions, à savoir: Arctic zone, Subarctic forest zone, Hardwood forest zone, Carolinian zone, The Prairie, Rocky Mountain foothills, Rocky Mountains proper, Selkirk Range, The Coast Range, Vancouver Island, Dry Belts of British Columbia. Il faut noter que les "zones" des auteurs sont de vastes régions phytogéographiques, mais non les zones géographiques circumpolaires.

Pour Villeneuve (130), qui s'inspire surtout de Thornthwaite (123, 124, 125), le Québec se divise, au point de vue climatique, en trois "types": le type tempéré, qui correspond à la zone tempérée classique, la taïga, qui comprend tout l'espace entre les zones tempérée et arctique, enfin la toundra, correspondant à la zone arctique classique.

Dans la péninsule Québec–Labrador, je distingue, du sud au nord, les zones suivantes (Fig. 2): (1) Au sud du 50° lat. N., la zone tempérée. (2) Du 50° au 55°, la zone subarctique. (3) Du 55° au 58° la zone hémiarctique. (4) Au nord du 58°, la zone arctique. Les limites mentionnées sont évidemment approximatives.

Pour simplifier le problème, l'étude de la zone hémiarctique suivra celle des zones arctique et subarctique. Il n'y sera pas question de stratification en altitude, bien que celle-ci, jusqu'à un certain degré, répète la stratification latitudinale.

La zone tempérée dans le Québec ou le Québec tempéré

Les caractéristiques

Il n'est pas nécessaire de décrire par le menu la végétation de la zone tempérée du Québec. La zone tempérée du Québec, telle que considérée ici, est le secteur que Marie-Victorin (65) et Raymond (85) nomment *région laurentienne*, que Hustich (45) divise en *southern spruce forest* et en un secteur innommé,—sans les englober dans une classe générale,—et que Hare (35), de

son côté, partage en *main boreal forest* et *southern transition zone*,—sans les englober non plus dans une classe générale.—Cette région, qui a fait l'objet des études phytogéographiques intéressantes de Marie-Victorin et de Raymond, comprend une forêt dense, à parterre couvert d'une riche végétation arbustive et herbacée. Dans la zone tempérée du Québec croissent environ 2000 espèces (contre environ 700 dans le zone subarctique du Québec–Labrador, 550 dans l'hémiarctique et 360 dans le Québec–Labrador arctique).

Dans le nord de la zone tempérée, la forêt conifériene comprend: *Picea mariana, Picea glauca, Larix laricina, Abies balsamea, Betula papyrifera, Populus tremuloides*, auxquels viennent s'ajouter, un peu plus au sud, *Pinus Strobus, Pinus resinosa, Thuja occidentalis*, puis, avec les formations de bois mêlé, *Tsuga canadensis, Betula lutea, Fagus grandifolia, Acer rubrum, Acer saccharophorum, Fraxinus americana*, etc. Dans la partie la plus boréale de la zone tempérée, la forêt conifériene est parfaitement exploitable, non clairsemée, comme le sera la forêt subarctique, et son sol n'est pas recouvert d'un tapis de *Cladonia*. Ces notions élémentaires suffiront pour distinguer la zone tempérée des autres, mais, comme nous le verrons plus loin, ce n'est pas la seule caractéristique.

Régions de la zone tempérée

L'emploi du concept de "zone tempérée" dans la phytogéographie de l'Amérique du Nord,—contrairement à la pratique de Merriam, Harshberger, Marie-Victorin, Halliday (33), etc.—oblige à décaler certains termes employés par ces auteurs pour des catégories subordonnées. La première catégorie subordonnée à la *zone* devrait être la *région*, ou la *province*, si l'on veut garder le mot région pour des entités inférieures; mais pour les besoins du présent travail j'ai choisi *région* parce que, très souvent, dans l'état actuel de nos connaissances, il n'est pas possible de fixer les provinces phytogéographiques. Je n'énumérerai pas ici toutes celles du Québec tempéré. Il suffira de mentionner, dans la partie supérieure du Québec tempéré, de l'ouest à l'est: la *région abitibienne* ("région de l'Abitibi" de Raymond ou, en partie, "*enclave argileuse Ojibway*" de Marie-Victorin), la *région laurentide* ("district laurentidien" de Marie-Victorin) et la *région saguenayenne* (Côte-nord). L'adjectif *laurentide*, appliqué à la région des Laurentides, remplace avantageusement le mot *laurentidien*, sans compter qu'il a déjà une forme adjective. Pour l'étude de la phytogéographie du Québec tempéré, voir Halliday, Hustich et surtout Marie-Victorin et Raymond (33, 45, 63, 65, 85). E. L. Braun (8) donne une excellente description de la végétation de la zone tempérée.

Limite de la zone tempérée au nord

Il importe toutefois de préciser la frontière boréale du Québec tempéré. Dans l'ouest du Québec, elle correspond au tracé de Hustich et Hare. Entre le 72° et le 70° long. W., comme j'ai pu m'en rendre compte par mes nombreux voyages au lac Mistassini, elle traverse ce lac, un peu suivant le tracé de la carte de Halliday. A l'est du 65° long. W., elle suit sensiblement le 51° 30′

jusque dans les parages de Mingan. Un travail manuscrit de R. N. Drummond, de McGill University, intitulé "A traverse of the Romaine river to establish ground control for the interpretation of aerial photographs, 1950" confirme cette vue. Le récit manuscrit du voyage du père Babel en 1866 par les portages de la rivière St-Jean jusqu'à la Romaine, placerait à 51° 15′ le début du subarctique dans ces parages. Cette divergence est probablement due simplement à une erreur dans la détermination de la latitude sur les vieilles cartes qui ont servi à l'interprétation du récit de voyage. Au-delà des îles Mingan, vers l'est, Marie-Victorin, Halliday et Hare,—qui dans ce secteur se répètent sensiblement,—font passer la ligne trop au nord à mon avis. C'est du moins ce qu'il m'a semblé après avoir traversé plusieurs fois la région en avion. Cela n'exclut pas la possibilité d'avant-postes tempérés dans la zone subarctique; mais ils ne sont peut-être pas aussi généreux que sur les tracés de Halliday et Hare. En effet, les parages de Goose Bay, qui d'après Hare constitueraient un avant-poste tempéré (*outlier of main boreal forest*), renferment des forêts à sous-bois de *Cladonia*, caractéristiques des forêts subarctiques. Les photos 189 et 190 de Tanner (122) sont particulièrement convaincantes. Il est juste toutefois de noter que la forêt est particulièrement dense auprès des cours d'eau, quand, sur le plateau sablonneux, quelques centaines de mètres plus loin, elle s'éclaircit au point de ressembler à un parc. Ce qui dans de minimes secteurs de ce territoire rend la forêt dense et lui donne une importance économique, c'est l'humidité et la présence de sédiments riches. Sur la Kaniapiskau et au lac Mistassini, des roches dolomitiques supportent également une forêt luxuriante. Dans la forêt subarctique, se trouvent ici et là de telles parcelles forestières, que les conditions locales d'humidité, de protection et de composition du sol ont favorisées. Ainsi sur la Koksoak, comme sur la rivière George, la forêt est certainement plus luxuriante à cinquante kilomètres de la baie d'Ungava qu'elle ne l'est à l'intérieur de la péninsule.

La zone subarctique dans la péninsule Québec–Labrador ou le Québec et le Labrador subarctiques

La zone subarctique du Québec comprend d'abondants lacs, de grandes tourbières, subissant très fréquemment le phénomène de la solifluxion, et des forêts clairsemées. Les lacs ont une flore beaucoup plus pauvre, en espèces et en individus, que ceux de la zone tempérée. La tourbière de la zone subarctique a perdu quelques éléments, mais par contre d'autres les remplacent. Toutefois la présence de parcelles tourbeuses ne peut suffire pour caractériser une zone entière; car si les tourbières sont essentiellement des habitats d'allure arctique-subarctique, elles sont extrêmement nombreuses dans la zone tempérée. Elles y constituent alors partiellement des avant-postes des zones du nord. Dans la zone subarctique, la tourbière n'est pas plus continue que dans la zone tempérée. Plus que le lac et la tourbière, la forêt ou parc subarctique est un élément permettant de caractériser d'un premier coup d'oeil la zone.

Le parc subarctique ou taïga

La forêt subarctique est essentiellement un parc aux arbres espacés (Fig. 3, 4). L'épinette noire (*Picea mariana*) est de beaucoup le plus important. Il occupe au-delà de 95% de la forêt. Presque toujours de petite taille, les spécimens les plus caractéristiques ont de cinq à dix mètres de haut. Exceptionnellement ils ont plus de quinze mètres. Les mélèzes (*Larix laricina*) abondent surtout en bordure des rivières et des lacs. Fréquemment ils y constituent une file d'un vert tendre qu'on ne peut manquer de remarquer en survolant le territoire. A Fort-Chimo, par exception, le *Larix laricina* est le principal arbre des collines; mais ceci est peut-être dû au fait que les Esquimaux et les Naskapis, occupant le territoire depuis un temps immémorial, ont pratiquement éliminé les formations de *Picea mariana* pour en faire du combustible. Ils laissent systématiquement de côté les mélèzes parce que,—m'ont affirmé des Esquimaux et des Naskapis,—le bois de cette espèce est trop lourd. L'épinette blanche (*Picea glauca*) occupe (sur la rivière George du moins, mais il est absent de la Korok), la même aire que le *Picea mariana*, mais c'est toujours un arbre très rare qu'on distingue de loin par sa taille, très élevée par comparaison avec l'épinette noire. Le peuplier baumier (*Populus balsamifera* var. *subcordata*) forme de minuscules bocages disséminés. J'en ai vu jusqu'au voisinage de la zone arctique, sur la rivière George, par 58° 30′ N. Toutefois ce serait une erreur de faire passer là la limite nord de l'aire de l'espèce. Dans l'hémiarctique il n'y en a que des avant-postes et c'est avant tout une espèce des zones tempérée et subarctique. Le sapin (*Abies balsamea*) est toujours disséminé dans le subarctique et sa limite nord correspond grosso modo à celle de la zone. Turner (in Ms.), qui a exploré la région de Fort-Chimo au siècle dernier, cite l'*Abies balsamea* comme très répandu à cet endroit, mais je n'en ai pas vu. Le tremble (*Populus tremuloides*) et le bouleau à papier (*Betula papyrifera*) semblent entièrement absents du territoire de la rivière George. Hustich et Hare font passer trop au nord la limite de l'aire générale du *Betula papyrifera*. Ces deux arbres toutefois ne sont pas entièrement absents de la zone subarctique, où ils sont relativement abondants dans le sud (sections S4, S5, S14 décrites plus loin). La seule présence de *Betula papyrifera* à Richmond Gulf (dans la zone hémiarctique) ne suffirait pas pour faire de cet arbre une espèce caractéristique de toute la zone subarctique. En effet, autant qu'on en peut juger par les récoltes faites à Richmond Gulf par Lepage et Dutilly (19, 20), il semble y avoir là un avant-poste tempéré. J'ai vu également le *Betula papyrifera* sur la Kaniapiskau et la Korok (2 secteurs hémiarctiques, N^{os} H5 et H9), mais il s'agissait là d'avant-postes. Dans l'ouest de la péninsule, la forêt subarctique peut également héberger le *Pinus Banksiana*, l'aire de cette espèce étant limitée par des conditions édaphiques. Ce qu'il faut retenir, c'est que la forêt subarctique est avant tout un parc de *Picea mariana*, avec *Larix laricina* en bordure des cours d'eau, et que ces arbres sont généralement de petite taille, partant, de pauvre valeur économique.

L'étage arbustif est bien caractéristique. Dans les parcs secs de la rivière George, dans la zone subarctique, on rencontre notamment:

Betula glandulosa
Chiogenes hispidula
Empetrum nigrum
Ledum groenlandicum
Ribes glandulosum
Salix discolor
Sorbus decora
Vaccinium angustifolium
Vaccinium cespitosum
Vaccinium uliginosum s. l.
Vaccinium Vitis-Idaea var. *minus*

Les parcs humides, par contre, renferment surtout:

Betula glandulosa
Chamaedaphne calyculata
Kalmia Polifolia
Ledum groenlandicum
Rubus acaulis
Rubus Chamaemorus
Salix cordifolia var. *callicarpaea*
Salix pedicellaris var. *hypoglauca*

Aux listes précitées, on pourrait ajouter le *Betula borealis*, plutôt rare, habitant surtout des clairières relativement sèches, l'*Alnus crispa*, fréquentant plutôt la berge des rivières, et le *Juniperus communis* var. *depressa*, des habitats secs, mais fréquemment absent de grands secteurs.

A noter que le sous-bois du parc subarctique est envahi par des arbustes qui, dans la zone tempérée, se limitent aux tourbières où aux collines de quartzite plus ou moins dénudées. Ainsi les *Kalmia Polifolia*, *Chamaedaphne calyculata*, *Ledum groenlandicum*. D'autres arbustes, qui dans la zone subarctique fréquentent la forêt aussi bien que la tourbière, habitent plutôt, dans la zone tempérée, les habitats découverts des berges et certaines tourbières. C'est le cas particulièrement de l'*Empetrum nigrum* et du *Vaccinium uliginosum*; mais il ne faut pas oublier que cette dernière espèce n'habite, dans la zone tempérée, que des avant-postes subarctiques ou arctiques. Le *Betula glandulosa*, le *Sorbus decora*, le *Rubus Chamaemorus* et le *Rubus acaulis*,—qui fréquentent un peu les forêts les plus au nord de la zone tempérée,—sont avant tout des arbustes subarctiques et presque des indicateurs de cette zone.

De beaucoup les arbustes les plus fréquents de la forêt subarctique sont les *Betula glandulosa*, *Empetrum nigrum*, *Rubus Chamaemorus* et *Vaccinium Vitis-Idaea* var. *minus*. Le groupement de ces quatre espèces et de l'épinette noire (*Picea mariana*), dans les parcs secs, et des mêmes espèces, moins l'*Empetrum* et le *Vaccinium*, dans les parcs humides, suffit presque pour caractériser la zone subarctique.

Les arbustes minuscules sont des éléments importants du tapis végétal subarctique. Leur rôle s'accroît encore dans les zones hémiarctique et arctique. Malgré leur apparence herbacée superficielle, le *Rubus Chamaemorus*, le *R. acaulis* et même le *Salix herbacea* sont bien des arbustes, comme en témoigne leur structure.

Plus remarquable encore le tapis herbacé des parcs ou forêts clairsemées, très variable suivant le type forestier. Dans la péninsule Québec–Labrador,

Hustich (45, 46 *b*) distingue dix types de forêts, depuis le *conifer lichen forest* jusqu'au *rich swamp forest*, repartis en trois séries différentes, les *dry series*, *moist series* et *wet series*. Pour les fins du présent travail, il suffit de distinguer les types extrêmes, le parc sec et le parc marécageux. Le parc sec a un tapis de *Cladonia* (*Cladonia gracilis*, *C. digitata*, *C. impexa*, *C. deformis* et autres espèces apparentées au *C. alpestris* et au *C. mitis*); le parc humide renferme un tapis de *Sphagnum* (notamment *S. recurvum*) fortement imbibé.

Ceux qui ont survolé le parc subarctique sec n'oublient pas facilement ces grands tapis de *Cladonia* blanchâtre, que transpercent des arbres dispersés, et qui semblent de vastes étendues de neige. Vu de près, ce tapis est un tissu assez compact, se fendillant en dalles polygonales par temps secs. Lorsque le matin la rosée imbibe encore la végétation, il ne reste plus trace des *polygones lichéniques*: à leur place se trouve une nappe continue. Le matin, le tapis de lichens est spongieux et obéit au pas comme une éponge, mais dès que le soleil de la matinée l'a desséché, il devient cassant comme des efflorescences cristallines et se broie sous les pas en crissant (107).

À ce tapis lichénique s'ajoutent quelques mousses, surtout dans les endroits les plus ombragés. On y trouve notamment:

Calliergonella Schreberi
Hypnum crista-castrensis
Mylia anomala
Polytrichum commune
Polytrichum juniperinum

et également d'autres lichens, *Cladonia rangiferina*, *Nephroma arcticum*, etc., et des champignons, notamment *Boletus scaber*, *B. versipillis* ou des espèces apparentées encore mal comprises.

À part les arbustes déjà mentionnés, les plantes phanérogames traversant le tapis lichénique sont plutôt rares. Elles comprennent notamment:

Carex deflexa
Cornus canadensis
Coptis groenlandica
Linnaea borealis var. *americana*
Luzula parviflora var. *melanocarpa*
Lycopodium annotinum var. *pungens*
Lycopodium complanatum
Lycopodium Selago
Mitella nuda
Moneses uniflora
Pyrola grandiflora
Pyrola minor
Solidago macrophylla
Trientalis americana
Viola labradorica

Parmi ces espèces, les plus caractéristiques sont probablement *Cornus canadensis*, *Deschampsia flexuosa*, *Linnaea borealis*, *Lycopodium annotinum* et *Solidago macrophylla*.

Les principaux associés phanérogamiques de la forêt sphagneuse sont:

Carex gynocrates
Carex pauciflora
Castilleja septentrionalis
Dryopteris spinulosa
Eriophorum angustifolium
Pyrola secunda var. *obtusata*
Ranunculus lapponicus
Streptopus amplexifolius

Ces communautés sont celles de la région de la rivière George. Elles varient quelque peu avec les divers secteurs subarctiques et la composition chimique du sol. C'est ainsi que les parcs humides recouvrant des sols

dolomitiques peuvent héberger des formations de *Salix vestita*. Si l'on voulait caractériser par une formule simple le parc subarctique on pourrait le définir: une formation d'épinettes noires (*Picea mariana*) de petite taille et espacées, avec sous-bois arbustif de *Betula glandulosa* et *Rubus Chamaemorus* et sol recouvert d'un tapis de *Cladonia* (type *alpestris*) ou de *Sphagnum*, selon qu'il s'agisse d'un parc sec ou d'un parc humide.

Ce type de forêt clairsemée ou de parc est la taïga, taïga sèche ou taïga humide, selon le cas. Hare (35), dans son étude très intéressante sur le climat et les types forestiers, s'objecte au terme taïga, "since the latter is applied by Russian ecologists to the entire formation and is so understood by geographers everywhere". Lors du congrès international de botanique à Stockholm en 1950, j'ai consulté à ce sujet plusieurs écologistes finlandais parlant le russe; aussi il ne me semble pas que l'opinion précitée soit générale. Que la taïga désigne soit le parc subarctique proprement dit, soit la formation entière, ne complique aucunement le problème. C'est une question de contexte. Il existe d'ailleurs beaucoup d'autres exemples à l'appui. La *steppe* peut être, suivant le point de vue, une formation écologique ou un secteur. La *toundra*, pour le géographe, le phytogéographe, le météorologiste, l'économiste, etc., comprend la "prairie" arctique avec ses cours d'eau, ses lacs et ses tourbières; pour l'écologiste, la toundra est un type défini de plaine arctique. Pour le géographe, l'économiste et le phytogéographe, la *forêt boréale* comprend la forêt proprement dite, avec ses lacs, ses cours d'eau et ses habitats les plus variés; pour le forestier et l'écologiste, la *forêt conifèrienne boréale* est une entité boisée bien définie. Pour le géographe, le *désert* englobe à la fois un habitat d'une excessive aridité et ses oasis; pour l'écologiste, *désert* et *oasis* sont des entités différentes. De même, le terme *taïga* peut s'appliquer, tantôt à toute la région couverte par la forêt subarctique, tantôt à la forêt elle-même. Dans tous ces cas les termes ont des acceptions différentes selon le point de vue. Peut-être en viendra-t-on finalement à donner à chacun un sens unique; mais comme le contexte permet toujours de distinguer clairement, il y a peu d'avantage à proposer un terme nouveau. D'ailleurs, s'il fallait distinguer nominalement la forêt proprement dite de la région, l'ancien terme de *forêt subarctique* conviendrait beaucoup mieux que celui de forêt ouverte boréale ou forêt clairsemée boréale (*open boreal woodland*). D'autre part, la distinction que Hare fait entre *forest* ("forêt dense") et *woodland* ("forêt à arbres espacés") n'enlève pas l'équivoque. *Woodland* signifie aussi *boisé* (adjectif ou nom). Le *boisé* (comme en anglais *woodland*) peut donc évoquer la petite forêt d'importance économique, l'annexe forestière de la ferme. Or il existe des boisés clairsemés et des boisés denses. S'il faut substituer à *forêt* un terme mieux approprié, *parc* l'emporte sur tout autre, du moins en français. Comme équivalent anglais on me suggère *parkland*, ce qui semble la meilleure solution.

Le climax

Décrivant les types forestiers, Hare constate que "many of them are definitely not "climax" and probably represent successional stages that must

soon give way to a higher form of forest" (35). Il est indéniable que la forêt renferme des parcelles qui ne sont pas rendues au climax, mais à des stades de succession. Cela se produit surtout quand une forêt a été détruite par l'homme, l'incendie, les épidémies et certains facteurs physiques à comportement subit. Dans la partie subarctique du Québec, l'exploitation forestière ne peut être en cause. Lorsqu'une forêt y évolue vers le climax, c'est qu'elle a été d'abord détruite par des agents tels que l'incendie. Par le contexte, il est évident que ce n'est pas le point de vue de l'auteur. Sans envisager de destruction récente, l'auteur est d'avis que certaines de ces forêts évoluent néanmoins vers un climax: "it may well be that there has not been time since the Wisconsin glaciation for the forest to attain its climax tree line" (p. 631). Si j'ai bien compris le point de vue de l'auteur, cette façon d'envisager le climax, bien qu'assez courante chez les botanistes, donne une extension qu'il ne devrait pas avoir. En effet, le temps écoulé depuis la glaciation Wisconsin est tel que toute la région a eu normalement le temps d'atteindre le climax. Si les conditions climatiques ont varié, c'est autre chose: il y a *changement de climax*, donc *clisère*. Clements, cité par Cain (11), s'exprime ainsi au sujet de tels cas: "The clisere represents a sequence of climaxes that moves as a unit in the face of climatic changes." D'ailleurs, la définition que Clements (12) donne du climax est assez nette. Cain (11) la résume ainsi: "The climax constitutes the major unit of vegetation and it is regarded as synonymous with formation and biome; it is considered a more or less permanent and *final stage of a complex organism under the paramount control of climate*." E. L. Braun (8), de son côté, écrit: "A climax (. . . .) is reached, when *under existing climatic conditions, no further change is possible*, because the reactions of the occupying dominants prevent the entrance of new forms".

Hare m'a fait part, dans une communication personnelle, qu'il avait en vue une série de climax, donc une clisère, lorsqu'il écrivit la phrase précédemment citée. Il s'agissait donc d'un remplacement de climax, non d'un climax théorique atteint à la suite de changements à l'échelle géologique.

Si j'avais à préciser mon interprétation du climax, je le définirais même: "Le *stage ultime de l'évolution* d'une formation végétale donnée, *dans un habitat et un climat donnés*. Cette interprétation nous rapproche évidemment beaucoup plus du polyclimax de DuRietz, Gams, Nordhagen et autres que du climax de Clements. Pour ce dernier (voir notamment Cain (11)), le climax est l'*unité principale* de végétation rendue à un stade définitif, par suite des conditions climatiques prévalentes. A l'intérieur du climax, Clements reconnaît des groupes subordonnés, des sortes de climax de seconde zone, par exemple les lociations et faciations, qui n'ont pas droit au nom de climax. Si on les considère sous l'angle spatial, il ne peut être question de climax, puisqu'il ne s'agit pas de l'unité dominante, mais biologiquement, ces communautés en sont, puisqu'elles ont atteint le stade ultime de leur évolution pour le climat et le sol ambiants. D'autre part, elles ne sont pas réductibles à l'unité principale. Considérés selon l'angle biologique, la forêt et le lac

des Laurentides appartiennent chacun à un climax différent. J'admets bien toutefois avec Cain que les interprétations des tenants du polyclimax et du monoclimax diffèrent surtout par la terminologie. Toutefois, pour la description des changements climatiques dans les zones arctique et subarctique, le système du polyclimax me semble se prêter à plus de clarté, sinon de logique. Ainsi, avec cette interprétation, le climax, à un endroit, est le parc de *Picea mariana*, avec sous-bois de *Betula glandulosa* et de *Cladonia*. Ailleurs, là où le terrain est normalement humide, le climax peut être le bosquet de *Picea mariana* avec sous-bois de *Betula glandulosa* et *Sphagnum recurvum*. Sur une colline dépourvue de végétation arborescente, le climax sera peut-être une communauté où domine le *Salix herbacea*. Bien plus, dans l'étage subalpin, à la limite des arbres, où se fait sentir particulièrement l'action combinée du vent et de la gelée, le climax,—aussi paradoxal que cela soit,—peut être une formation déprimée de *Picea*. "Mais, dira-t-on, il existe de telles formations végétales qui sont évidemment en voie d'évolution. Ainsi, telle formation de *Picea* rabougris que l'on croyait fixée depuis toujours évolue maintenant vers la forêt normale parce que le climat se réchauffe. Telle formation de *Salix herbacea* ou de *Salix Uva-ursi* disparaîtra devant l'envahissement des épinettes, par suite encore de la modification des agents climatiques. Bien plus, là où le "climax" était le glacier (effectivement un climax azoïque), se trouve maintenant un sol dépourvu de glace se couvrant lentement de *Phippsia algida*, de *Carex rufina* et de *Salix herbacea*". Cette évolution due au changement de climat,—les tenants des deux systèmes l'admettent,—n'est pas un indice que les habitats n'avaient pas atteint leur climax biologique, mais signifie simplement que le climax lui-même se déplace. Or pour décrire les différentes étapes du changement, qui seraient permanentes si le climat s'arrêtait à un palier donné, il est plus facile d'invoquer des climax parallèles et différents que des catégories subordonnées, revêtues d'une terminologie compliquée. Toutefois, je tiens à signaler que l'expression de ce point de vue sur le problème du climax n'est ici qu'une question accessoire qui ne change en rien les données et les conclusions du présent travail.

Limites de la zone subarctique (Fig. 2)

Mon point de vue n'est pas diamétralement opposé à celui de Hare. A part cette précision sur le climax, il n'en diffère guère que par des divergences plutôt minimes sur quelques aspects onomastiques et sur le tracé précis de la frontière des zones. Ces dernières, à la vérité, seront connues avec précision seulement quand l'intérieur de la péninsule aura été exploré davantage. Jusque là, il y a place pour la spéculation. Il est possible certes d'utiliser la photographie aérienne pour déterminer la limite des groupements forestiers, mais il faut alors le concours de botanistes avertis connaissant déjà de visu la flore des territoires. Les limites proposées par Hustich, Hare et moi-même, et qui sont grosso modo les mêmes, conviennent raisonnablement, à quelques détails près. Elles s'accordent d'ailleurs assez bien avec les courbes de la température efficiente (*thermal efficiency*) de Thornthwaite dont Hare (35) donne un bon aperçu. L'essai de corrélation entre le climat et les groupes

forestiers justifie pleinement l'établissement des zones biologiques telles que comprises (mais avec une terminologie différente) par Hustich, Hare et moi-même.

Les courbes de la température efficiente de Thornthwaite (123, 124, 125), toutefois, infirment l'opinion de Hustich considérant comme subarctique, non pas la taïga, mais le territoire au nord de la taïga. Ce point reviendra sur le tapis lors de l'étude de la zone hémiarctique.

La limite de la zone subarctique et de la zone tempérée a été esquissée sommairement dans le chapitre sur la zone tempérée. Hustich a basé le tracé de la limite nord de la taïga continue,—la zone subarctique telle que comprise ici,—en partie sur les travaux de Marr (67) et de Jacques Rousseau.[4] Hare a adopté la même ligne, en annexant toutefois à la taïga proprement dite le territoire de la partie inférieure de la rivière Kaniapiskau, comme Hustich l'avait fait dans son étude détaillée des groupes forestiers (45). Il est possible qu'il faille adopter cette ligne de conduite, mais en l'absence d'une étude de la partie inférieure de la Kaniapiskau, il me semble préférable de l'exclure de la taïga et de l'annexer à la toundra forestière. L'ayant survolée en 1951 j'ai pu me rendre compte que seul le voisinage immédiat de la rivière bénéficiait d'une certaine luxuriance.

Les régions de la zone subarctique de la péninsule Québec–Labrador

Sans infirmer la classification des groupes forestiers de Hustich (45), il y a lieu néanmoins de proposer des régions artificielles plus restreintes pour fins d'inventaire floristique. On connaît encore très mal la zone subarctique du Québec. D'ici à ce qu'on établisse avec une approximation raisonnable la distribution de sa flore (ce qui permettra alors d'aborder la structure même de la végétation), il vaut mieux limiter les régions aux bassins hydrographiques, sauf lorsqu'elles sont bien caractérisées phytogéographiquement. Les divisions proposées sont les suivantes:

S. 1. Région orientale de la baie James (Eastern James Bay region).—Cette région s'étend à une cinquantaine de milles à l'intérieur (parfois une trentaine seulement) et s'arrête avec les derniers dépôts glacio-marins. Cette région, déjà reconnue par Halliday (33) et Hustich (45), a été étudiée botaniquement par Potter en 1932 (82, 83), Margaret T. Doutt (17),[5] Gardner en 1930 et 1933 (30, 31), Lepage et Dutilly entre 1943 et 1945 (18, 19, 20, 21), Hustich, Tuomikoski, Kucyniak et Baldwin, en 1947 (46).

S. 2. Région Grande-rivière – Kanaaupskow (Grand-River – Kanaaupskow region).—Bassin hydrographique de ces deux rivières, à l'arrière de la région S. 1, et du cours supérieur de la Great Whale. La Grande-rivière se nomme parfois rivière Fort-George. Cette région n'a jamais été explorée sauf en une courte visite de Hustich sur la Great Whale (46).

S. 3. Région de l'Eastmain (Eastmain region).—Portion du bassin hydrographique de l'Eastmain, à l'est de la région S. 1. Inexplorée au point de vue botanique.

[4] *Verbatim et in litteris.*
[5] *Les plantes récoltées toutefois n'ont pas encore été identifiées.*

S. 4. Région de la Rupert (Rupert River region).—Comprenant le bassin hydrographique de la Rupert, depuis la limite de la région S. 1, jusqu'au lac Mistassini. Explorée par André Michaux en 1792 (102, 117), Macoun en 1885 et 1887 (58, 59), Dutilly et Lepage en 1943 (18).

S. 5. Région du lac Mistassini (Lake Mistassini region). (Fig. 3)—Sauf l'extrémité sud-ouest, la région du lac Mistassini est subarctique. Territoire exploré par André Michaux en 1792 (102, 117), Macoun en 1885 (59, 58), Lepage et Dutilly en 1943 (18), Rousseau, de 1944 à 1948 (accompagné par Ernest Rouleau en 1944). Les travaux de Rousseau et Rouleau sont encore manuscrits.

S. 6. Région des monts Otish (Otish Mountains region).—À la hauteur des terres, au sud du lac Nichikun. Cette région à sommets alpins a été explorée par Rousseau et Pomerleau en 1949. Résultats partiels publiés (52*a*, 81*a* 112*a*).

S. 7. Région du lac Kaniapiskau (Kaniapiskau lake region).—Bassin du lac Kaniapiskau et de la rivière Kaniapiskau dans la partie supérieure du cours. Cette région se rend grosso modo à la ligne de partage des eaux au sud. Au nord, cette région est bordée par la région de la rivière Kaniapiskau, dans la zone hémiarctique. Entièrement inexplorée, sauf les environs de Knob Lake, dans le coin nord-ouest, visités par Hustich en 1948 (46*a*) et Rousseau en 1951.

S. 8. Région des lacs Michikamau et *Hubbard* (Lake Michikamau – Lake Hubbard region).—Région située au nord du bassin de la rivière Hamilton. Elle comprend la partie supérieure de la rivière Naskapi et la source de la rivière George. Région inexplorée, sauf la source de la rivière George par Rousseau en 1947 (103, 105, 110, 112). Pour caractériser la zone subarctique dans le Québec, l'auteur s'est basé notamment sur la partie supérieure du lac Mistassini (S. 6) et une partie de la présente région (S. 8).

S. 9. Région de l'Hamilton supérieur (Upper Hamilton river region).—Partie occidentale d'une région déjà caractérisée par Hustich (Hamilton river section) (45). Inexplorée botaniquement, sauf les herborisations de A. R. A. Taylor, au lac Panchia en 1944, et de Hustich, dans les environs de Knob Lake, en 1948 (46*a*). A noter que Knob Lake se trouve à la frontière des régions S. 7 et S. 9 et également de la région H5 de l'hémiarctique.

S. 10. Région des lacs Attikonak et Ashuanipi (Attikonak–Ashuanipi Lakes region). (Fig. 4)—Entre le bassin de la rivière Hamilton, celui du Lac Kaniapiskau, et la ligne de partage des eaux au sud. Région inexplorée, sauf une très courte herborisation d'A. R. A. Taylor au lac Sawbill, en 1944.

S. 11. Région de la rivière Canairiktok (Canairiktok Region).—Bassin hydrographique de la Canairiktok entre la côte de l'Atlantique et le bassin de la rivière Hamilton. Inexplorée botaniquement.

S. 12. Région de l'Hamilton inférieur.—Partie orientale d'une région déjà caractérisée par Hustich (voir S. 9). A fait l'objet d'explorations sommaires notamment par Wetmore (134). Pour description, voir Kindle et Tanner (50, 122).

S. 13. Région des rivières à l'Aigle et Kénamou (Kenamou and Eagle Rivers region).—Entre le bassin de la rivière Hamilton et la ligne frontière Québec–Labrador au sud. Inexplorée botaniquement.

S. 14. Intérieur de la côte Nord du Saint-Laurent et rive à l'ouest de Mingan.—Vaste région s'étendant du fleuve Saint-Laurent à la hauteur des terres ou à la frontière sud du Labrador. Comme la rive du golfe est surtout arctique, j'ai rattaché à l'hémiarctique la côte à l'est de Mingan (voir H10). L'intérieur de cette région, qu'il importera probablement de diviser, n'a jamais été exploré. Il renferme notamment de vastes avant-postes arctiques. Bien que la fig. 2 ne l'indique pas, il faut rattacher à la région S. 14 une partie de la rive du Saint-Laurent, à l'ouest de Mingan. Cette côte a été visitée par Saint-Cyr en 1883 et 1885 (113, 114, 115), Harold St-John en 1915 (116),[6] Marie-Victorin en 1923 (63, 65, 66) et Harrison Lewis de 1927 à 1930 (55), et autres.

Avant-postes subarctiques

Il s'en trouve plusieurs dans la zone tempérée. C'est le cas notamment des tourbières partiellement boisées. Les véritables avant-postes arctiques sont beaucoup plus évidents. Toutefois, ces derniers sont bordés, le plus souvent, d'une bande subarctique. Pour l'énumération des principaux avant-postes, voir plus loin.

La zone arctique dans la péninsule Québec–Labrador ou le Québec et le Labrador arctiques

Il semblerait plus logique à première vue de décrire la zone hémiarctique avant de passer à l'arctique, puisqu'elle se place entre le subarctique et l'arctique; mais il est plus facile de la caractériser après une étude sommaire des deux autres zones.

Les géographes et climatologistes, depuis Nordenskiöld (72, 73), décrivent l'arctique comme une zone où la moyenne du mois le plus chaud de l'année ne monte pas au-delà de 10° C. (50° F.). Cet isotherme est naturellement basé sur une période normale,—une vingtaine d'années—. Autrement, il faudrait parfois rejeter de l'arctique d'immenses territoires. C'est le cas de l'année 1948. Du 15 juillet au 15 août, lors de la traversée de la péninsule de l'Ungava par les rivières Payne et Kogaluk, l'auteur n'a relevé que deux nuits où la température descendit à 0° C. Très souvent, la nuit, elle se tenait un peu au-dessus de 10° C. Le jour, elle atteignit même 31° C. (88° F.). Sans aucun doute, si l'on avait basé sur cette année là seulement l'isotherme de 10° C., il aurait passé plus au nord.

L'arctique est une région où le permafrost (7, 84) se rencontre le plus souvent à moins d'un mètre de profond, souvent même à 50 cm. L'arctique est donc une masse de glace (ou un rocher à la température de la glace), couverte d'un tapis de sol qui dégèle l'été et supporte alors une maigre

[6] *St. John donne un excellent aperçu de tous les travaux antérieurs.*

végétation. Le sol est l'objet de divers mouvements réunis sous le nom de *cryoperturbation*. Cela comprend notamment la *solifluxion*, les *sols polygonaux* et les *ostioles* (107).[7]

Pour le biologiste, la zone arctique est avant tout une vague prairie dépourvue d'arbres et même de conifères arbustifs, sauf exceptionnellement le *Juniperus communis* déprimé. Cette prairie arctique est la *toundra* (Figs. 10, 11).

Toundra et tourbière

Le mot toundra s'emploie dans deux sens. C'est d'une part une région entière, avec ses lacs, ses marécages, ses tourbières, la berge des cours d'eau, les platières sablonneuses ou graveleuses, la zone intercotidale et surtout une vaste prairie gazonnante, comprenant des plantes herbacées, des arbustes rabougris, des lichens et des mousses. Le mot toundra a aussi un deuxième sens, beaucoup plus limité, celui d'un habitat particulier, la prairie arctique gazonnante dont il vient d'être question. Pour les géographes, climatologistes, ethnographes et les voyageurs en général, la toundra comprend tout le territoire arctique, sauf les étendues maritimes. Pour l'écologiste et l'auteur de monographies floristiques, la toundra est l'habitat dominant de la toundra-région. Comme pour la forêt boréale, le désert, la taïga etc., cette dualité de sens ne pose aucun problème. Le contexte indique assez clairement qu'il s'agit de la toundra-région ou de la toundra-habitat. Il n'y a donc pas lieu de les distinguer par des termes différents; la multiplication des termes différents pour désigner des concepts aussi étroitement apparentés contribue peu à l'avancement des connaissances et ne fait souvent qu'embrouiller des idées qui autrement seraient claires. S'il fallait absolument distinguer l'habitat de la région, pourquoi ne dirions-nous pas simplement la toundra-habitat et la toundra-région. Que nous le voulions ou non, les deux sens existent; il faut se résoudre à en tirer le meilleur parti.

Pour le non-initié, la toundra peut ressembler superficiellement aux prairies des zones tempérée et tropicale, ou au désert. La prairie de l'ouest du Canada, dans la zone tempérée, a remplacé la mer crétacée et éocène. La composition chimique du sol, notamment, s'opposant à la croissance des arbres, il en est résulté de grandes formations herbeuses. Dans le Yucatan, et dans la zone subtropicale en général, l'incendie répété des formations forestières ou frutescentes pour défricher le sol aboutit à un type d'habitat dégradé, une prairie herbeuse irréversible. Le défrichement par brûlage, dans l'agriculture iroquoise, a produit dans la région de Montréal des "prairies" arbustives renfermant de grandes formations d'aubépines (*Crataegus*) et a sans doute favorisé la création de nouvelles espèces dans ce vaste genre en crise de mutabilité. Non seulement des facteurs édaphiques, mais également des facteurs climatiques ont présidé, sans doute, à la formation des prairies précédentes. Les déserts,—à part les oasis aux points d'eau et les dunes arides,—hébergent une végétation clairsemée, formée de plantes herbacées et

[7] *Pour l'étude de tous ces phénomènes voir les travaux suivants (10, 38, 107, 127, 132) qui donnent l'ensemble de la bibliographie.*

d'arbustes. La photographie des prairies, de secteurs de déserts et de la toundra peut certes présenter des similitudes. La toundra diffère néanmoins des prairies tempérées ou tropicales et des déserts par de nombreux facteurs. Le système des saisons est différent: la toundra bénéficie d'un été d'un mois ou deux seulement, entrecoupé par des gelées et des chutes de neige. Les moyennes de température et leurs variations annuelle et quotidienne n'ont rien de commun avec celles des autres zones. Le système d'irrigation spontané diffère essentiellement: l'eau de la toundra, venant surtout de la fonte de la neige et du sol gelé au cours de l'hiver, au-dessus du permafrost, a un débit normal pendant toute la saison de végétation. Dans le désert, le système radiculaire peut atteindre parfois cinq à dix mètres de profond; dans l'arctique il ne peut guère descendre à plus de cinquante centimètres. S'il ne rencontre pas le permafrost à ce niveau, l'eau glacée qui y circule n'est guère favorable à sa croissance. Le jour-lumière de l'arctique est extrêmement long en été,—parfois 24 heures même,—quand celui des zones tempérée et tropicale est alors de douze à dix-huit heures tout au plus. Les facteurs lumière, température et eau n'ont donc pas le même comportement, dans l'arctique d'une part, dans la prairie tempérée et le désert tropical d'autre part. Il n'est donc pas surprenant que la flore de la toundra diffère entièrement de celle de ces habitats.

Où le problème paraît plus complexe, c'est dans la comparaison de la toundra et de la tourbière. La tourbière de la zone tempérée, pour une partie intéressante de ses éléments floristiques, est un avant-poste arctique ou subarctique. Peut-être serait-il plus juste de dire que la tourbière de la zone tempérée est un refuge habituel d'éléments arctiques et subarctiques. Il y voisine donc des éléments arctiques et tempérés. Elle n'est pas l'équivalent de la toundra, même si elle a avec celle-ci une certaine parenté. Léandri (54), à la suite de von Bulow, considère la toundra comme une sorte de tourbière recevant son eau du sol sous-jacent. C'est un fait que la toundra et la tourbière tempérée ont plusieurs éléments floristiques en commun, comme le *Ledum groenlandicum* et d'autres Ericacées. Si, pour caractériser une tourbière, on s'en remettait seulement à certaines Ericacées, il faudrait placer avec les tourbières les collines de quartzite de Kamouraska, dans la province de Québec, où le *Ledum groenlandicum* et le *Kalmia angustifolia* croissent sur des rochers secs. Les collines de quartzite sec, situées entre Guysborough et Canso, en Nouvelle-Ecosse, hébergent également ces arbustes, accompagnés de plantes acidophiles qu'on trouve d'habitude dans les tourbières. C'est le cas des *Drosera rotundifolia*, *D. intermedia*, *Viola lanceolata* et même du *Sarracenia purpurea*, quand ce dernier peut s'établir dans de petites dépressions rocheuses retenant un peu d'eau,—parfois un demi-litre seulement,—ce qui est assez pour permettre à une touffe de *Sphagnum* de se développer (98). Si quelques plantes acidophiles ne font pas la tourbière, un sous-sol de matière organique n'est pas suffisant non plus pour la caractériser. Une forêt mal drainée permet l'accumulation de terreau noir; pourtant on ne l'assimile pas à la tourbière. Une tourbière est un habitat mal égoutté, couvert d'associa-

tions floristiques assez élaborées, différant par de nombreux éléments de la flore de la toundra et formant des dépôts de tourbe s'accroissant d'année en année. Or, c'est dans le nord de la zone tempérée que les tourbières semblent atteindre leur optimum. La tourbe s'accroît en épaisseur parce que les débris organiques ne se décomposent pas entièrement dans l'eau acide. Lorsque la tourbière s'accroît plus au centre qu'au bord et forme une espèce de dôme, la matière organique est assez spongieuse pour retenir de l'eau dans ses mailles, même dans les parties situées au-dessus du niveau de la nappe d'eau normale.

La tourbière est donc essentiellement un habitat humide, dont le sol organique s'accroît normalement en épaisseur. La toundra est aussi en partie un habitat humide, parce que l'eau de la couche active du sol, dégelant au cours de l'été, circule au-dessus du permafrost. La surface de la toundra, par contre, est fréquemment sèche et plus exposée à l'oxydation que la tourbière imbibée. C'est sans doute pour cela que la tourbe ne s'y accumule pas comme dans la tourbière. La surface de la toundra supporte un tapis à peu près continu de lichens,—notamment de *Cladonia alpestris*, *C. mitis* ou d'espèces apparentées, *Alectoria*, *Stereocaulon*, etc.,—qui sont incontestablement des éléments d'habitats secs. Si l'on voulait caractériser ces habitats au moyen d'une formule simple (et peut-être un peu trop simplifiée) on pourrait affirmer que la toundra est revêtue d'un tapis de lichens, et la tourbière d'un tapis de *Sphagnum*. Evidemment il faudrait tenir compte des éléments phanérogamiques. Tous ceux qui ont parcouru la toundra savent que ses formations de *Saxifraga*, de *Dryas*, de *Vaccinium Vitis-Idaea*, de *Ranunculus*, de *Caryophyllacées*, sans compter les *Arabis*, *Draba*, *Eutrema* et autres, ne lui donnent aucunement l'allure d'une tourbière. Dans la tourbière comme dans la toundra se rencontrent les *Ledum*, *Kalmia*, *Chamaedaphne*, *Eriophorum*. C'est que ces plantes, émergeant du tapis sec de la surface de la toundra, sont profondément enracinées dans la couche d'humus sous-jacente, couche toujours liquide et fortement acide. Si la toundra diffère de la tourbière par les plantes de la surface, elle s'en rapproche donc par celles qui sont enracinées profondément.

N'allons pas croire que la vraie tourbière est absente de l'arctique. Dans les endroits les plus humides, on trouve effectivement de minuscules tourbières ressemblant à celles de la zone tempérée, compte tenu des éléments appartenant à une zone plutôt qu'à l'autre.

Ultérieurement, nous examinerons plus en détails la couverture végétale de la toundra. Pour le moment, le fait de savoir que la zone arctique est caractérisée par la toundra,—une prairie végétale reposant sur un sol glacé et dépourvu d'arbres,—suffit pour la séparer des zones tempérée et subarctique. La zone arctique, faut-il le rappeler, est floristiquement pauvre. Quand le Québec subarctique compte trois fois moins d'espèces que le Québec tempéré, le Québec arctique en compte six fois moins.

Limite de la zone arctique au sud (Fig. 2)

Ce point sera étudié dans le chapitre sur la zone hémiarctique. Toutefois l'on peut affirmer pour le moment que cette limite passe grosso modo aux environs du 58° de lat. N.

Les régions de la zone arctique de la péninsule Québec–Labrador (Fig. 2)

Pour le moment on peut distinguer une dizaine de régions géographiques définies.

A. 1. Région Wolstenholme – Wakeham Bay.—Extrémité nord-ouest de la province de Québec, cette région comprend tout le triangle nord-ouest de l'Ungava, au nord du 60° de latitude, donc le triangle Povungnituk – cap Wolstenholme – Cape Hopes Advance. La limite sud est donc une ligne allant du 60° sur la rive de la baie d'Hudson, à 60° 30′ sur la baie d'Ungava. Dans ce territoire, où la principale rivière est la Povungnituk, que le géologue Flaherty (27) a parcourue en 1912, et les rivières secondaires la Kovic et la Wakeham, il n'y a eu d'explorés que les rares points de la côte touchés par les vaisseaux et dont Polunin donne la liste (79), et le lac McGill à l'intérieur, où Polunin fit une herborisation lors d'une escale d'hydravion. Il faudrait peut-être diviser cette région en deux régions au moins,—versant de la baie d'Hudson (rivière Povungnituk et Kovic), versant du détroit d'Hudson et de la baie d'Ungava (des environs d'Iviguvik aux environs de Cape Hopes Advance),—mais cette solution semble prématurée, vu la pauvreté de nos connaissances. Payne a fait dans ce secteur des observations botaniques que Lawson a relevées (53). Dans ce secteur se trouve le cratère de l'Ungava (cratère Chubb), exploré géologiquement par V. B. Meen et F. W. Chubb (68), en 1950 et 1951, et où J. Rousseau fit une excursion botanique en 1951 (68).

A. 2. Région de la Kogaluk (Fig. 10 et 11).—Appartenant au système hydrographique du versant de la baie d'Hudson, entre le 60° N. et la limite des arbres au nord du lac Minto. La principale rivière de cette région est la Kogaluk, d'environ cent cinquante kilomètres de longueur, explorée pour la première fois par l'auteur en 1948 (104, 105, 110).[8] Auparavant, les zoologistes Todd (126) et Doutt avaient visité la rivière à environ 35 kilomètres au-dessus de l'embouchure. Port-Harrison, dans la partie sud du territoire, étant l'unique port d'escale des navires dans ces parages, avait déjà reçu la visite de quelques botanistes, notamment Malte en 1928 et 1929, Gardner entre 1930 et 1933, Polunin en 1936, et quelques autres. Une monographie de la flore de la région de la rivière Kogaluk, par Jacques Rousseau et Marcel Raymond, est actuellement en préparation. (Voir aussi 81*b*, 112*b*.)

A. 3. Région de la rivière Payne.—Dans le bassin hydrographique de la baie d'Ungava entre le 60° 30′ lat. N. et la limite des arbres quelques milles au nord de la rivière aux Feuilles (Leaf River). La plus importante rivière du nord-ouest de l'Ungava (avec la rivière aux Feuilles), la rivière Payne, a sa source dans le lac Payne, long d'environ cent kilomètres. Le géologue

[8] *L'auteur avait pour compagnons Edgar Aubert de la Rue, géologue, Philippe Michéa, ethnologue, et Pierre Gadbois, géographe. Ils ont publié depuis les travaux 5, 6, 29.*

Flaherty (27) a exploré la partie inférieure de la Payne (à l'est de la rivière Flaherty, ou North Payne Branch), en 1912, et Ney et Courtright ont fait une herborisation autour du poste de Payne Bay en 1936, mais la rivière a été explorée entièrement pour la première fois en 1948 par Jacques Rousseau et son groupe (104, 105, 110, 87). Les résultats de l'exploration botanique des rivières Kogaluk et Payne font l'objet d'une monographie par Rousseau et Raymond, actuellement en préparation. (Voir aussi 81*b*, 112*b*.)

A. 4. Côte sud de la baie d'Ungava.—La rive de la baie d'Ungava est dépourvue d'arbres sur une bande étroite. La ligne des arbres, passant quelques milles au nord de la rivière aux Feuilles, s'incurve donc au sud et longe la côte de la baie d'Ungava à quelques milles à l'intérieur des terres, passant approximativement à mi-chemin entre l'embouchure de la Koksoak et le poste de Fort-Chimo sur cette rivière. Cette région est inconnue sauf les îles Naujats, visitées par l'auteur en 1947 et l'embouchure de la rivière aux Feuilles, visitée par Marr en 1948. (Matériaux identifiés par Marcel Raymond.)

A. 5. Région de Port-Burwell.—Extrémité N.E. de la péninsule Québec–Labrador jusqu'aux îles Button inclusivement. La plus grande partie de ce territoire est dans la province de Québec, notamment Port-Burwell, un ancien poste de la Hudson's Bay Co., maintenant abandonné depuis quelques années. Région explorée notamment par Hantzsch en 1906 (34, 121). Pour liste des plantes récoltées aux environs de Port-Burwell, un ancien port d'escale des vaisseaux visitant l'arctique, voir Polunin (79).

A. 6. Région des Torngat.—Située au sud-est de la région A. 5, cette région comprend le massif des Torngat et les montagnes au sud jusqu'au voisinage de Nain. Des massifs montagneux du Québec, près de la hauteur des terres, sont également dans cette région. Les Torngat ont été explorés géologiquement par Coleman (13), et botaniquement par Abbe (1, 2). Delabarre (14), Malte, Gardner (30, 31), Polunin, Wynne-Edwards (137) et d'autres,[9] ont herborisé à certains points d'escale. Jacques Rousseau s'y rendit en 1951, traversant l'extrémité nord-est de l'Ungava et du Labrador, en partant de la baie d'Ungava. Tanner et Hustich (41, 44, 45, 47, 48, 122) ont également étudié la végétation d'une partie de cette région. La frontière de ce secteur et de la région A. 7, dans le nord, est la ligne frontière des deux provinces. Au voisinage de la Korok, elle empiète très légèrement (environ 15 kilomètres) sur le bassin de cette rivière dans le Québec. Plus au sud, elle englobe toute la partie arctique du Québec, à l'ouest de la frontière interprovinciale et appartenant au bassin de la George. Le centre de la section A. 6, dans le sud, est basé sur les cartes de Hustich et Tanner. Dans certaines baies, entre Hebron et Port Manvers, se trouvent des avant-postes de la forêt subarctique. On doit considérer ces baies comme faisant partie de la région H. 8 de l'hémiarctique. Pour régler un aspect orthographique, je me permets d'ajouter que Torngat est le pluriel esquimau de Torngak. Les deux graphies s'emploient.

[9] *Beaucoup de travaux se rapportent plus ou moins à l'ensemble du Labrador, Sections A. 6 et H. 8. Voir notamment les travaux cités pour section H. 8.*

A. 7. Région du fjord Adloylik.—Au sud-ouest de la région de Port-Burwell (A. 5) et à l'ouest de la partie nord de la région des Torngat (A. 6). La région A. 7 a été explorée au cours de l'été 1951 par Jacques Rousseau. Ce fjord se nomme parfois, à tort, sur les cartes, fjord Abluviak.

A. 8. Île Mansel.—Appartenant administrativement aux territoires du Nord-ouest, mais sa proximité de la péninsule Québec–Labrador demanderait qu'on la traite avec cette province. Île peu explorée. Pour les récoltes faites sur l'île Mansel, voir Polunin (78, 79).

A. 9. Région des îles Belchers.—Cette région comprend les îles de la partie orientale de la baie d'Hudson, depuis le 60° lat. N. jusqu'au cap Jones à l'entrée de la baie James, et notamment les îles Belchers. Région peu explorée qu'ont visitée, à quelques points, Gardner (30, 31), Dutilly et Lepage (19, 20). Ces îles, pour fins administratives, appartiennent aux territoires du Nord-ouest; mais leur flore doit être traitée avec celle du Québec.

A. 10. Île Akpatok.—Grande île de la baie d'Ungava, appartenant administrativement aux territoires du Nord-ouest, explorée par Polunin (74, 75, 76, 77).

La zone hémiarctique dans la péninsule Québec–Labrador ou le Québec et le Labrador hémiarctiques

La toundra forestière: caractéristique de la zone hémiarctique (Fig. 5-9)

La toundra est caractérisée notamment par l'absence complète d'arbres. Le parc subarctique,—ou taïga, telle que définie précédemment,—est une forêt sans valeur économique, aux arbres petits et clairsemés, à sol couvert d'une formation presque continue de lichens, surtout de *Cladonia*. Entre la toundra continue et la taïga continue, dans la péninsule Québec–Labrador, se trouve une vaste bande d'environ quatre cents kilomètres de large où des parcelles toundriques alternent avec des parcelles taïgales (Fig. 5, 6). Nous le verrons plus loin, ce n'est pas un intermédiaire entre la taïga et la toundra, mais une mosaïque des deux, où chaque élément garde son originalité. Plus précisément, le fond des vallons et la berge des cours d'eau sont occupés par d'étroites bandes taïgales pendant que les légères élévations, à cinq ou dix mètres environ du niveau de l'eau, sont le plus souvent occupées par des parcelles toundriques (Fig. 5, 8). Il ne faut pas croire cependant, comme on me l'a suggéré, que ces parcelles toundriques doivent leur origine à l'incendie de la forêt subarctique. Il est vrai que les parcelles subarctiques incendiées, dans le nord de la zone hémiarctique, restent souvent désertes, mais on les distingue bien des parcelles toundriques naturelles. Cette espèce d'*habitat composite* a reçu le nom de toundra forestière. Il ne faut pas perdre de vue l'aspect composite. En réalité, les parcelles toundriques de la toundra forestière sont un habitat et les parcelles boisées de la toundra forestière, un autre habitat bien distinct (plus exactement plusieurs autres habitats distincts). Quand une telle mosaïque de parcelles boisées et non boisées se

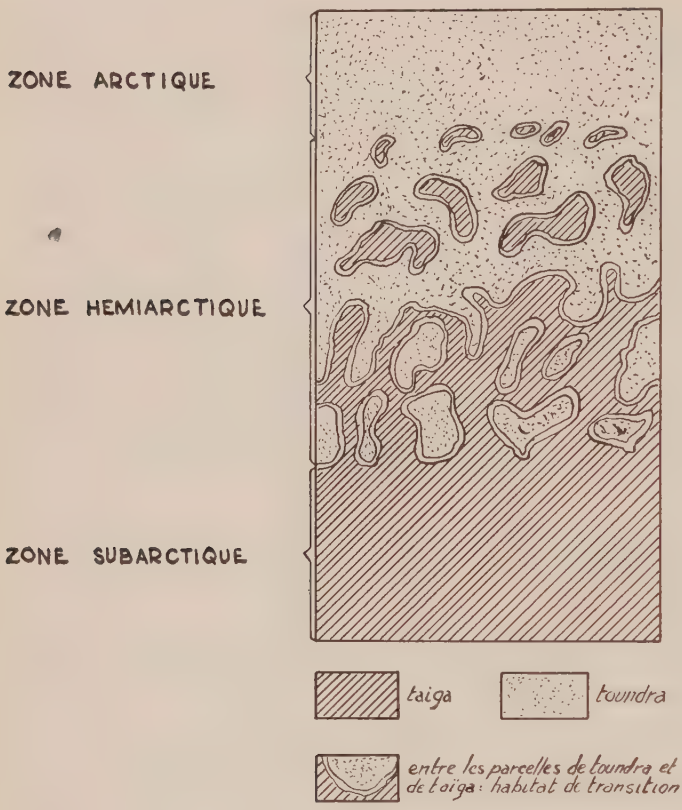

FIG. 1. Représentation schématique des zones arctique, hémiarctique et subarctique, avec indication (en blanc) des étroites bandes de transition entre chaque parcelle arctique et chaque parcelle subarctique. La zone hémiarctique se présente comme une émulsion des zones arctique et subarctique.

répète sur l'étendue de trois degrés de latitude, il est bien justifiable de créer un terme pour la caractériser: *toundra forestière* (*forest tundra*) désigne donc une mosaïque d'habitats, non un habitat autonome.

Si l'on excepte quelques parcelles de toundra alpine dans la taïga, le passage de la taïga à la toundra forestière est assez abrupt, comme j'ai pu le noter sur la rivière George, dans l'est de l'Ungava. Le territoire au sud de 55° 5′ lat. N. est couvert par la taïga typique. Au 55° 5′ lat. N. apparaît sur une colline la première parcelle de toundra. Ces parcelles augmentent rapidement en nombre jusqu'au 55° 9′ lat. N. Au nord de ce point, la taïga est restreinte au fond des vallées et au bord des cours d'eau et ne couvre pas en étendue plus de vingt-cinq pour cent du territoire. Dès le 55° 10′ lat. N., les parcelles de toundra se fraient parfois un chemin jusqu'aux cours d'eau.

La zone *hémiarctique* est une association d'habitats franchement arctiques et d'habitats franchement subarctiques. Au lieu d'être une "solution", un mélange parfait des deux zones, donc un type intermédiaire, c'est une "émulsion" de deux zones (Fig. 1). La zone hémiarctique est donc aux zones

arctique et subarctique ce que la toundra forestière est à la toundra et à la taïga, un élément essentiellement composite. A cause de celà, d'aucuns trouveraient préférable, sans doute, de placer la toundra forestière toute entière dans la zone subarctique. Solution peu logique à la vérité. Probablement plus de 75% de la zone hémiarctique est de caractère arctique; s'il fallait renoncer à la zone hémiarctique, la seule solution serait d'annexer à l'arctique tout le territoire situé sur la rivière George entre 55° 9′ et la limite absolue des arbres. Il faudrait alors indiquer par des signes conventionnels la multitude des îlots subarctiques. Plus pratique me semble l'adoption de cette zone composite que justifient d'ailleurs pleinement les données climatiques, comme nous le verrons dans un chapître ultérieur. Et si l'on accepte cette zone composite, le qualificatif d'*hémiarctique*,—signifiant "*à demi arctique*" (dans le sens d' "*en partie arctique*"),—me semble approprié. Cette notion de zone hémiarctique a été proposée par l'auteur à une réunion de la Société Royale du Canada en juin 1949, mais il n'avait encore paru sur le sujet qu'un court résumé (106; voir aussi 108*a*).

Si, ce que je nomme zone hémiarctique n'est pas simplement un habitat de transition entre le subarctique et l'arctique, cela ne signifie pas qu'il n'y a pas d'habitats de transition entre la taïga et la toundra. Cette transition se trouve effectivement à la périphérie de chaque parcelle de forêt subarctique (Fig. 1). Elle comprend notamment, sur une bande de quelques pieds, des *Picea mariana* de type junipéroïde (surtout *Picea mariana* f. *empetroides* Marie-Victorin et Rousseau).

Pour certains, ces épinettes junipéroïdes, à la périphérie des parcelles taïgales, sont un indice de la régression de la forêt. Au contraire, la présence dans les parcelles boisées de grands *Picea mariana* à branches retombantes serait une indication que la forêt est en voie de s'étendre. Ceci se justifie peut-être dans certaines régions subalpines du sud,—ce que j'ignore,—mais pas dans l'immense zone hémiarctique de l'Ungava. Dans tous les secteurs de la zone hémiarctique visités, les parcelles boisées étaient entourées d'une étroite bande d'épinettes junipéroïdes; par contre, le centre des formations comptait le plus souvent des arbres à branches retombantes. Les deux types se rencontraient parfois à deux ou trois mètres de distance. L'épinette à branches retombantes doit peut-être parfois son existence à des facteurs écologiques, mais il est indéniable que des facteurs génétiques peuvent être souvent en cause. Plusieurs de ces formes se propagent effectivement dans les pépinières.

La discussion précédente prend pour acquit que la taïga est essentiellement subarctique. De cette opinion sont également Harshberger (37), Marie-Victorin (65), Villeneuve (130) et d'autres. Hustich (45) toutefois présente une vue différente: "The taiga and the southern spruce forest subregion form the boreal forest region. The *forest–tundra area* (including forest patches and barren grounds) *should* according to the author's opinion *be called the Subarctic region.* [Les italiques sont de Hustich.] The term or expression "Subarctic" has been used in various meanings. If this expression could be

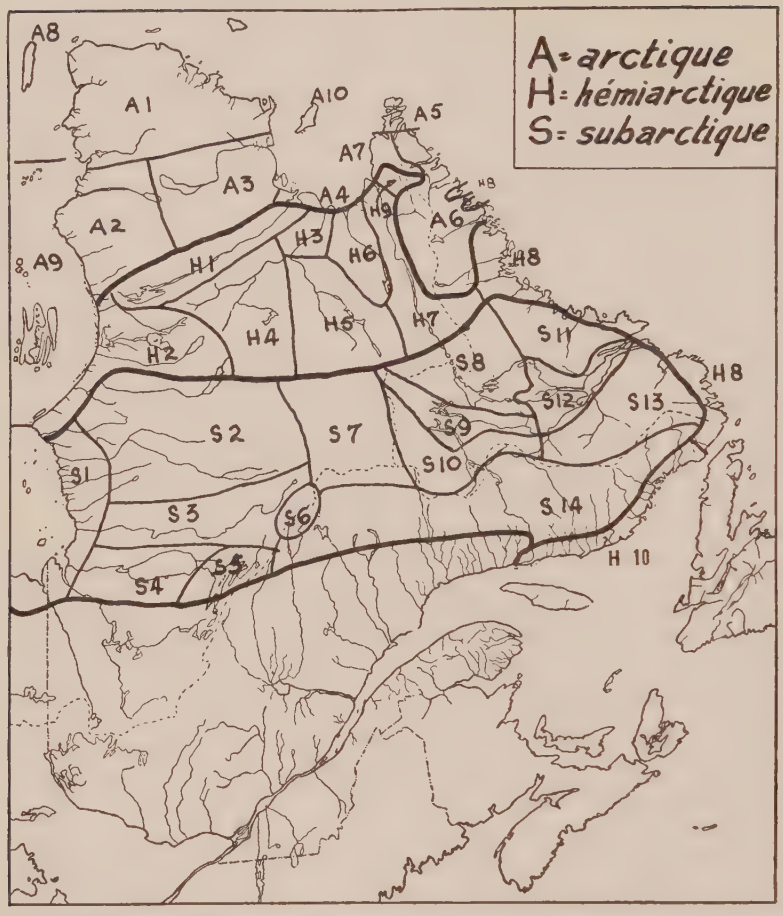

FIG. 2. Les zones biologiques de la péninsule Québec–Labrador, avec subdivisions des zones arctique, hémiarctique et subarctique.

restricted to comprise only the belt between the boreal forest region and the arctic region, i.e. the forest–tundra as defined here, it would serve to clarify our vague phytogeographical terminology". Si l'on ne considérait que les arbres eux-mêmes, cette solution serait partiellement acceptable, mais il faudrait néanmoins placer la taïga dans la zone subarctique, puisque les types d'arbres et la couverture lichénique du sol de la taïga continue et des parcelles forestières de la zone hémiarctique sont les mêmes. On a rencontré le permafrost dans la taïga, au sud du 55° lat N. (49). La taïga, telle que délimitée par Hustich, se trouve entièrement au nord de l'isotherme de 32° F. (ou 0° C.) pour l'année (32). Ces considérations seules, qu'appuient d'ailleurs les courbes de Thornthwaite (35), suffiraient pour placer la taïga dans la zone subarctique. D'autre part une étude comparée des éléments floristiques de la taïga et de la forêt tempérée n'est pas moins convaincante. Ne considérons pour le moment que l'aspect statistique. Le Québec tempéré, moins étendu

que le Québec–Labrador subarctique (dans le sens où je l'entends), compte environ 2000 plantes vasculaires, contre environ 700 dans le Québec–Labrador subarctique (la taïga délimitée par Hustich). Il est vrai que le subarctique n'a pas été entièrement exploré, mais les dernières explorations révèlent que la découverte d'espèces nouvelles se fait maintenant à un rythme aussi lent chez lui que dans la partie tempérée et qu'elle ne modifiera pas sensiblement la proportion d'un tiers.

Limites de la zone hémiarctique (Fig. 2)

La limite au nord est la ligne des arbres. Extendons par là la limite absolue des arbres (même réduits au port arbustif) et non le "timberline" qui est la ligne frontière des arbres à "taille d'arbre". Les deux sont sensiblement parallèles et rapprochées. Entre le "timberline" et la ligne absolue des arbres (*tree line*), il ne reste plus que des conifères rabougris que l'on placerait avec les arbustes si la forme typique n'avait un port arborescent. Ce secteur très étroit est un secteur de transition. De même que l'on passait assez subitement du subarctique à l'hémiarctique, de même l'on passe brusquement de l'hémiarctique à l'arctique. La limite nord du Québec–Labrador hémiarctique commence à la Pointe de la Baleine-Blanche, à l'est du lac Minto (par 57° 10′ lat. N. environ), se dirige vers le N.E. suivant une ligne parallèle à la rivière aux Feuilles, à environ 15-20 kilomètres au nord de la rivière. Cette ligne semble traverser la rivière aux Feuilles près de l'embouchure de celle-ci, dans le lac aux Feuilles (qui n'est pas un lac en réalité mais une baie estuarienne où se font sentir les marées de la baie d'Ungava), puis longer la baie d'Ungava à environ dix ou vingt kilomètres à l'intérieur des terres. Dans la région de la Koksoak, la zone arctique se rend à une vingtaine de kilomètres de la baie, près de Fort-Chimo. A la rivière à la Baleine, la zone hémiarctique se rend jusqu'au milieu de la petite baie évasée de l'estuaire. A la rivière Tuktuk, elle se rend au fond de la baie estuarienne (baie Aluptaluk). Après avoir traversé l'estuaire de la rivière George à une vingtaine de kilomètres de la baie d'Ungava, elle suit à quelque distance le rivage de la baie d'Ungava. Elle passe à environ un mille à l'est du fond de la baie de la Korok et va envelopper entièrement la rivière Korok jusqu'à 64° 15′ long. W., pour se recourber vers le sud-ouest. Elle longe ensuite la rivière George, quelques kilomètres à l'est et jusqu'aux environs du 56° N., pour se recourber vers le nord et se terminer aux environs de Nain, vers 56° 30′ N. Le grand lobe arctique du Labrador, à l'est de la rivière George, est basé surtout sur les cartes de Tanner et Hustich (45, 122), les photos aériennes et l'exploration de la George et de la Korok, par Rousseau, en 1947 et 1951.

On sait que les arbres manquent sur une bande de quelques kilomètres (de vingt à cinquante apparemment) à l'est de la baie d'Hudson et ceci jusqu'aux environs du 54° au sud. De même, presque toute la côte du Labrador est dépourvue d'arbres, depuis l'extrémité nord jusqu'à Blanc-Sablon et même au delà, vers l'intérieur du St-Laurent. Le concept de zone hémiarctique dispense de placer cette étroite bande dans l'arctique.

Plus imprécise encore que la ligne septentrionale de l'hémiarctique, la frontière méridionale de cette zone. Comme l'intérieur a été peu exploré, ce n'est que dans les parages de la rivière George qu'il est possible de la fixer avec précision. Comme nous l'avons vu plus haut, la frontière du subarctique et de l'hémiarctique traverserait la rivière George par 55° 9′ N. Pour le reste, jusqu'à la connaissance de faits plus précis, on peut accepter grosso modo la limite de la taïga et de la toundra forestière telle que tracée par Hustich (45), mais en la prolongeant le long de la rive nord du golfe St-Laurent jusqu'aux environs des îles de Mingan.

Les régions du Québec–Labrador hémiarctique

Etudiant cette zone au point de vue forestier, Hustich (45) reconnait deux divisions phytogéographiques principales: le "Koksoak forest–tundra section" couvrant la vallée de la Kaniapiskau et de la Koksoak, et "l'Ungava forest–tundra section" couvrant le reste de la zone. La raison invoquée par Hustich pour distinguer la Koksoak–Kaniapiskau du reste est la présence d'une végétation relativement luxuriante dans le secteur. Il semble même qu'elle soit due aux calcaires dolomitiques abondants dans la vallée. L'on distinguera sans doute plus tard d'autres régions phytogéographiques définies dans la zone hémiarctique, mais, pour le moment, il semble préférable de s'en tenir surtout dans les inventaires floristiques aux régions géographiques simples que sont les bassins hydrographiques. Les régions de la zone hémiarctique pourraient ainsi se ramener à dix principales.

H. 1. Région de la rivière aux Feuilles (Leaf river region).—S'étend depuis le lac Minto jusqu'au lac aux Feuilles, à quelques milles de la baie d'Ungava, c'est la région de contact de l'arctique et de l'hémiarctique dans l'ouest du Québec. La ligne des arbres la sépare des régions de la Kogaluk et de la Payne. En 1912, en hiver, le géologue Robert Flaherty (27) parcourut la rivière en traîneau, depuis la source jusqu'à l'embouchure. La partie inférieure de la rivière a été explorée botaniquement par John W. Marr en 1948. Les résultats sont encore inédits, mais l'auteur put consulter la collection complète des récoltes, identifiées par Marcel Raymond, du Jardin botanique de Montréal. En 1946, Polunin fit des herborisations au lac Gregory, par 58° 27′ N. et 70° 8′ ouest (80, 81).

II. 2. Région de Richmond Gulf (Richmond Gulf region).—Au voisinage de la baie d'Hudson et couvrant les bassins de la rivière Nastapoka, de Richmond Gulf et de Little Whale river (y compris sa source, le lac d'Iberville ou Upper Seal) et la côte de la baie d'Hudson jusqu'au voisinage de Fort George. Gardner a visité quelques points de la côte de cette région, avant 1938. Richmond Gulf a reçu la visite de Marr en 1939 (67), de Lepage et Dutilly, en 1944 (19, 20), et Polunin a visité un point du lac Bienville (autrefois Apiskagamish) en 1946 (80). Suivant le tracé de Hustich, la plus grande partie de la Grande rivière de la Baleine (Great Whale river)[10] se trouverait

[10] *On a traduit officiellement Great Whale river et Little Whale river par rivière de la Grande Baleine et rivière de la Petite Baleine. Les traductions me paraissent fautives. Il faudrait plutôt, Grande rivière de la Baleine et Petite rivière de la Baleine.*

dans le subarctique, tandis que l'embouchure et la partie boréale du lac Bienville, à la source, serait dans l'hémiarctique. Ce dernier point ne semble faire aucun doute, car j'ai vu les photographies prises par Polunin au lac Bienville et Hustich, accompagné de Tuomikoski, Kucyniak et Baldwin, ont herborisé à l'embouchure en 1947 (46). D'après les récoltes de Dutilly et Lepage, il me semble que Richmond Gulf renferme un avant-poste tempéré.

H. 3. Région de la Koksoak (Fig. 5, 6) (Koksoak region).—Ceci comprend le bassin de la Koksoak, depuis le confluent des rivières Kaniapiskau et aux Mélèzes, et s'étend jusqu'à la ligne des arbres, quelques kilomètres au nord du poste de Fort-Chimo. C'est dans cette région que se trouve le poste de Fort-Chimo et l'aéroport de Fort-Chimo,—"la porte de l'arctique de l'est",—connu pendant la guerre comme Chrystal I, d'où le nom mentionné sur des étiquettes d'herbier. Presque tous les botanistes visitant un point de l'Amérique arctique orientale font un court séjour à Fort-Chimo. C'est néanmoins une région botaniquement complexe, presque toujours étudiée superficiellement, et sur laquelle pourtant chaque voyage apporte des précisions nouvelles. La père Arthème Dutilly et l'abbé Ernest Lepage, se rendant de Richmond Gulf à Fort-Chimo, en compagnie de Pierre Dagenais, en 1944, ont herborisé sur la Koksoak (19, 20), suivis de Polunin, en 1946 et 1949, Rousseau, en 1947, 1948 et 1951, J. W. Marr, H. Senn et J. A. Calder, en 1948. Antérieurement quelques gérants de postes de la Hudsons' Bay Company de même que l'ethnologue Turner (documents manuscrits, 128, 129, 22) avaient fait de maigres récoltes à Fort-Chimo. Tous ces résultats, encore inédits, font pour la plupart l'objet d'une publication imminente de Rousseau et Raymond. (Voir aussi 108*b*.)

H. 4. Région du lac à l'Eau-Claire et de la rivière aux Mélèzes (Stillwater–Larch region).—C'est le district situé entre ceux de Richmond Gulf, de la Koksoak, de la Kaniapiskau et de la rivière aux Feuilles. En 1944, Lepage et Dutilly firent un relevé botanique de la région, lors de leur traversée de Richmond Gulf à Fort-Chimo. Le journal de leur voyage a paru, de même que la liste de leurs récoltes (19, 20).

H. 5. Région de la Kaniapiskau (Kaniapiskau region).—Cette région comprend le bassin hydrographique de la Kaniapiskau, depuis son confluent avec la rivière aux Mélèzes (Larch river), jusqu'à la frontière de la taïga vers 55° N. Nous connaissions vaguement la forêt de la région par les explorations du géologue Low (56). Hustich a fait quelques herborisations dans l'extrémité sud de la région, à Knob Lake, en 1948. L'auteur a eu l'avantage d'examiner les collections de Hustich et de consulter son travail manuscrit, longtemps avant qu'il ne paraisse (46*a*). Rousseau a visité la même région en 1951. Toute la région de la Kaniapiskau, la mieux connue de l'Ungava au point de vue géologique, est encore à peu près inexplorée botaniquement. C'est pourtant l'une de celles qui promet le plus, si le travail est fait par des botanistes d'expérience. Survolant le voisinage de Fort Mackenzie, en 1951, il m'a semblé que certains lacs renfermaient des *Nuphar*.

H. 6. Région de la rivière à la Baleine (Whale river region).—La présence de trois rivières à la Baleine dans l'Ungava plaide peu en faveur de l'imagination toponymique des anciens voyageurs. Distinguons donc, pour éviter toute confusion, Little Whale river (petite rivière de la Baleine) et Great Whale river (grande rivière de la Baleine) se déversant dans la baie d'Hudson, et Whale River (rivière à la Baleine) se déversant dans la baie d'Ungava, à l'est de la rivière Koksoak. Dans la présente section H. 6, il faut placer les bassins hydrographiques de False river, de la rivière à la Baleine et toutes les petites rivières à l'est de cette dernière jusqu'aux environs de 66° 30′ long. W., mais à l'exclusion du rivage proprement dit de la baie d'Ungava, qui se place dans l'arctique. Région entièrement inexplorée, sauf une brève visite de Polunin à False River et au lac Ralleau en 1949. Ces matériaux n'ont pas encore été étudiés.

H. 7. Région de la rivière George (Fig. 7, 8, 9) (George river region).—Evitons de confondre la rivière George, qui se déverse dans la baie d'Ungava, et la rivière Fort-George, dans la baie James. Les deux témoignent d'un touchant loyalisme, mais sont néanmoins une source de confusion. La rivière George,—l'une des plus importantes de l'Ungava,—coule dans la zone hémiarctique depuis 55° 9′ lat. N. jusqu'à 58° 35′ N. approximativement. Cette région, visitée par Mme Hubbard en 1905 (39, 40), puis explorée botaniquement par Jacques Rousseau en 1947 (103, 105, 110, 52), fait l'objet de mémoires de Rousseau et Raymond (110, 112*c*, etc.) R. C. Clément, alors attaché au service météorologique de l'armée américaine, a herborisé au lac Indian House en 1944-1945. Ces derniers résultats, encore inédits, sont incorporés dans l'un des mémoires à venir de Rousseau et Raymond. (Voir aussi 81*b*.)

H. 8. Côte méridionale du Labrador (Southern Labrador Coast).—Cette région comprend approximativement les deux tiers de la côte du Labrador, depuis la baie d'Okkak jusqu'à Blanc-Sablon. On y trouve la plus grande partie des bassins des rivières Fraser et Assiwaban. Cette région n'est connue que par les herborisations,—d'ailleurs très nombreuses,—aux seuls ports d'escale, échelonnées sur un siècle et demi. Notons particulièrement les travaux suivants: Meyer (71), Schlechtendal (118), Ascherson (4), Butler (9), Macoun (61, 60), Fernald et Sornborger (26), Delabarre (15), MacKay (57), les récoltes de William MacGregor faites en 1905 et publiées en 1907 sans nom d'auteur (3), Fernald (23), Wetmore (134), Woodworth (136), Gardner (30, 31), Hustich et Pettersson (47, 48), Tanner (122) et Wenner (133). Ces auteurs ne sont pas tous allés sur la côte du Labrador. Certains ont basé leurs travaux sur les spécimens fournis par des collecteurs d'occasion. En dehors de l'aire principale de cette région, il faut lui rattacher des avant-postes subarctiques de la côte dans la région des Torngat (région A. 6) et qui sont désignées par le symbole H. 8′. Macoun (60) a fait un relevé des plantes cueillies par plusieurs voyageurs antérieurs, notamment W. A. Stearns. Bien que se rapportant à la section H. 10, St-John (116) donne une excellente bibliographie couvrant également la section H. 8, mais c'est surtout Tanner (122) qui est la principale source bibliographique.

H. 9. Région de la Korok. A l'ouest de la section A. 6 et au sud de A. 7. Wallace y est passé au cours de l'hiver 1906, mais n'a rien laissé d'intéressant sur la région (131). Wheeler, qui a suivi la Korok, également l'hiver, en a tracé la carte (135). Région explorée botaniquement par Jacques Rousseau en 1951 (108*c*).

H. 10. La côte Nord du St-Laurent entre Mingan et Blanc-Sablon.—La presque continuité de l'habitat arctique le long du fleuve exige que ce sècteur soit compris avec l'hémiarctique. Il a été visité par Saint-Cyr (113, 114, 115), Harold St-John (116), Marie-Victorin (63, 65, 66), Harrison Lewis (55), Fernald et Wiegand dans la région de Blanc-Sablon (23). Pour une bibliographie plus complète, voir surtout St. John (116) et Tanner (122).

Comparaison des divers habitats se retrouvant dans différentes zones

Pour caractériser les diverses zones climatiques, au moyen des formations végétales, on n'invoque habituellement que la couverture forestière et plus particulièrement l'association des espèces arborescentes. Ce point de vue, aussi pratique soit-il, n'est pas le seul et il est incomplet. La forêt, tout d'abord, ne comprend pas que des arbres, mais aussi des plantes frutescentes et herbacées. Ces dernières comptent des phanérogames, des bryophytes, des thallophytes. La forêt est, en réalité, une étroite association de plantes, d'animaux et d'hommes. Pour caractériser justement les zones climatiques et biologiques, il faudrait faire intervenir ces trois groupes d'êtres vivants, essentiels à l'établissement de toute classification biogéographique. Tant que l'on n'envisagera pas en entier le spectre systématique des êtres vivants, l'écologie et encore plus la biogéographie générale ne seront que des approximations.

On peut toutefois prévoir déjà que l'étude globale ne fera que répéter les conclusions des études particulières. Pour l'établissement des grandes zones biologiques, Merriam (69) avait eu recours surtout à la distribution des mammifères. La classification d'Harshberger (37), reposant sur quelques espèces végétales, précisait sensiblement la précédente. Tous les travaux postérieurs n'ont fait, dans les grandes lignes, que confirmer la première approximation de Merriam. Sans doute, les catégories choisies varient un peu et la frontière des zones évolue à mesure que s'étendent les connaissances.

Les limites tracées par Halliday (33), Hustich (45) et Hare (35) sont basées surtout sur la végétation arborescente. Dans les pages antérieures, j'ai tenu compte en outre du parterre forestier. En se basant uniquement sur la flore du parterre, on répartirait également le Québec en zones tempérée, subarctique, hémiarctique et arctique. Si l'on n'y recourt pas, la comparaison de la toundra aux secteurs forestiers pose toutefois un problème. Pour caractériser alors la zone arctique, il ne reste plus qu'un caractère négatif, l'absence de forêt.

Comme la zone arctique comprend seulement des habitats de pleine lumière, il y aurait avantage à comparer les habitats ouverts se retrouvant dans les

différentes zones: le lac, la tourbière, la grève marine, la berge et la grève des cours d'eau. Cette étude comparative, faite par Jacques Rousseau et Marcel Raymond et intitulée "Les habitats de pleine lumière et les zones biologiques", a dû, pour des raisons pratiques, être réservée pour une autre publication. Bien que sommaire, elle permet déjà de conclure que l'examen d'habitats très limités, dépourvus d'arbres, conduit aussi sûrement à l'identification des zones que la comparaison de la couverture arborescente. Cette méthode semble ouvrir un chapître fécond de la phytogéographie. Déjà, des travaux en cours de Marcel Raymond (86, 88) sur la distribution des *Carex* dans le Québec semblent indiquer que l'on pourrait arriver aux mêmes conclusions en se limitant strictement à un genre assez vaste. Pour toutes fins pratiques, les *Carex*, dans le Canada oriental, pourraient constituer le genre-clé des habitats et des aires phytogéographiques.

Les avant-postes arctiques et subarctiques

En dehors des zones arctique et subarctique proprement dites, se trouvent des parcelles qui, par leur composition floristique, appartiennent aux flores arctiques et subarctiques. Le plus simple est de les considérer comme des *avant-postes arctiques* ou *subarctiques*, en anglais, *arctic* et *subarctic outposts*.

Les avant-postes subarctiques

Ces avant-postes, dans la zone tempérée, sont d'identification plus difficile que les avant-postes arctiques. Assez souvent, les avant-postes arctiques sont séparés des habitats tempérés par une bordure subarctique qui constitue alors un avant-poste subarctique, mais souvent aussi il y a passage brusque de la parcelle arctique à la flore tempérée.

Tantôt,—et c'est le cas des tourbières boisées,—l'avant-poste est uniquement subarctique. C'est le cas probablement des forêts humides de la région de Valcartier hébergeant le *Ranunculus lapponicus*, certaines collines boisées du Bic, les petits taillis de *Pinus Banksiana* de Canso, en Nouvelle-Ecosse, et les tourbières littorales boisées de la rive sud-est de la Nouvelle-Ecosse étudiées par Rousseau (97, 98). Pour dresser la liste complète de ceux du Québec, il faudrait auparavant une étude plus détaillée de la couverture végétale.

Les avant-postes arctiques

Des parcelles des zones tempérée et subarctique se rattachent nettement à la zone arctique par leur flore. Ces habitats sont souvent arctiques-alpins plutôt que simplement arctiques. Il ne faut pas confondre les habitats arctiques et les alpins. Ce point fait l'objet d'une plus longue discussion ailleurs (109) et sera élaboré davantage dans une plus longue étude sur la flore des nunataks, actuellement en préparation. On peut considérer comme avant-postes arctiques tous les habitats naturels dépourvus d'arbres et recouverts d'une florule sensiblement semblable à celle de la toundra arctique. Les principaux avant-postes arctiques de la péninsule Québec–Labrador et des environs immédiats sont assez nombreux. Sans en esquisser ici la flore, il y a lieu néanmoins d'en dresser une liste préliminaire.

PA. 1. Des secteurs de Terre-Neuve. La flore de Terre-Neuve a été étudiée surtout par Fernald, qui a publié de nombreux mémoires sur le sujet dans *Rhodora*. (Voir notamment (23, 24, 25) et la liste compilée par Ernest Rouleau (89)).

PA. 2. Sommets des monts Otish, à la hauteur des terres, au sud du lac Nichikoun. Explorés botaniquement par Jacques Rousseau et René Pomerleau en 1949. Résultats d'ensemble à paraître. (Voir aussi 52*a*, 81*a*, 112*a*.)

PA. 3. Quelques secteurs de la zone subarctique au nord des Sept-Iles. Région inexplorée botaniquement; mais en survolant le territoire en avion, j'y ai distingué des parcelles de toundra arctique où la solifluxion agissait fortement.

PA. 4. Des secteurs du lac Mistassini. La flore du lac Mistassini a été étudiée particulièrement par Michaux, en 1792 (117, 102), Macoun (58), Dutilly et Lepage (18), Rousseau, de 1944 à 1947, accompagné de Rouleau en 1944 (Ms.).

PA. 5. Montagnes de St-Urbain, comté de Charlevoix. Explorées par Rousseau, en 1931 (91), Raymond et Kucyniak (51).

PA. 6. Rivières d'Anticosti et îles de Mingan. Explorées surtout par Marie-Victorin et Rolland-Germain, entre 1924 et 1928 (63, 65, 66), et quelque peu par Rousseau, en 1940 et 1942 (99, 108). Pour la bibliographie sur l'exploration d'Anticosti voir notamment les travaux de Rousseau (99, 108) et Raymond (86).

PA. 7. Côte de Gaspé.. Plusieurs points de la côte nord de la Gaspésie sont des habitats nettement arctiques. C'est le cas particulièrement de la côte, à la Tourelle, à la rivière à Claude, au Mont Saint-Pierre, à l'anse Pleureuse. Cette région a été explorée par Fernald, Marie-Victorin et Rolland-Germain, Rousseau et autres. Voir notamment Fernald (24), Marie-Victorin (63, 65, 66), Scoggan (119).

PA. 8. Monts Shikshok. Au centre de la péninsule de Gaspé. Explorés particulièrement par Fernald et également par Marie-Victorin et Rolland-Germain, Rousseau, Léopold Fortier, Louis-Marie, Raymond, Wynne-Edwards et autres. Voir notamment Fernald (24), Marie-Victorin (63, 66), Scoggan (119).

PA. 9. Certains points de la rive Nord de la baie des Chaleurs, dans le comté de Bonaventure. Région explorée surtout par Marie-Victorin et Rolland-Germain (64).

PA. 10. Rivières Matapédia et Restigouche. Explorées surtout par Rousseau en 1931 et plus tard par Le Gallo (90, 54 *a*).

PA. 11. Région du Bic, comté de Rimouski. Explorée par Fernald avant 1925, Rousseau en 1926, 1927 et 1936, Wynne-Edwards, en 1935 et 1936. La plupart des résultats, sauf quelques notes, sont inédits. Ils ont pu toutefois être incorporés en grande partie dans la liste de Scoggan. Voir surtout Fernald (24) et Scoggan (119).

PA. 12. Estuaire d'eau douce du Saint-Laurent. Exploré surtout par Marie-Victorin et Rolland-Germain, Rousseau (entre 1924 et 1935), Fernald

et Fassett. Il existe sur le sujet une bibliographie abondante. Pour une vue d'ensemble, voir Marie-Victorin (65). A ce secteur, Rousseau (93) donna le nom d' "*îlot subarctique*" qu'il fallut changer ultérieurement (109) en *avant-poste arctique.* Sur les plantes reliquales de l'estuaire voir les autres études de Rousseau (92, 94, 95, 96, 100, 101, 111).

PA. 13. Twin Islands, Baie James. Exploré botaniquement par Margaret Doutt (17) qui y a reconnu un avant-poste arctique. Résultats non publiés.

PA. 14. Iles de l'est de la baie James. Beaucoup de ces îles, depuis le sud de la baie jusqu'à la limite de l'hémiarctique au sud du cap Jones, hébergent une florule arctique d'après Hustich (46), qui en a exploré quelques-unes en compagnie de Tuomikoski, Kucyniak et Baldwyn. En attendant une étude définitive, il semble préférable de grouper toutes ces îles en un seul avant-poste.

PA. 15. Certains points des provinces Maritimes (autres que la rivière Restigouche). Notamment des secteurs de la rivière St-Jean. La liste des plantes arctiques du Nouveau-Brunswick a été dressée surtout par Fowler (28).

PA. 16. Mont Katahdin et autres habitats arctiques-alpins du Maine. Explorés notamment par Fernald (24). Sans doute faudrait-il distinguer aussi des avant-postes arctiques dans plusieurs estuaires du Maine.

PA. 17. Certains secteurs du Vermont. La rivière Winooski, plusieurs points de cet état, notamment Smuggler's Notch, ont révélé depuis fort longtemps des habitats arctiques-alpins. (Voir notamment Fernald (24) .) Il faudrait ajouter peut-être aussi quelques massifs du mont Sutton (province de Québec) continuant plus ou moins les montagnes du Vermont.

PA. 18. Mont Washington et autres secteurs arctiques-alpins du New-Hampshire. Il a paru de nombreux travaux sur la flore de ces montagnes. (Voir notamment Fernald (24)).

PA. 19. Massifs alpins des Adirondack. Notamment les monts Marcy et McIntyre.

PA. 20. Les tourbières de la zone tempérée jusqu'à un certain degré, sont des avant-postes arctiques et subarctiques (voir notamment Raymond (85)), en autant qu'elles servent de refuge à des plantes arctiques et subarctiques.

Il y aurait lieu aussi de signaler les avant-postes de la province d'Ontario, assez nombreux, et ceux des provinces de l'ouest, encore assez mal connus.

Conclusions générales

Les zones, interprétées au point de vue biologique, doivent pouvoir coïncider autant que possible avec les zones climatiques. Il est certain qu'on ne peut tracer autour du globe des cercles parallèles marquant leur limite, car elles sont influencées par le relief, les courants marins, froids ou chauds, les masses maritimes, le degré d'insolation, les courants atmosphériques, etc. En délimitant les zones au moyen des conditions physiques et faunistiques marines on arrive également à un décalage par rapport aux divisions terrestres. Il est possible également que la notion de zone hémiarctique ne se justifie

aucunement dans la vie sous-marine. Dans le travail qui nous intéresse présentement, la répartition des zones biologiques ne tient compte que des masses continentales et de la vie terrestre.

La plus intéressante étude de corrélation des zones climatiques et biologiques est celle de Hare (35),—et si je diffère de cet auteur sur des points de terminologie et des concepts écologiques, je n'en suis pas moins d'accord dans les grandes lignes avec son remarquable essai de corrélation.

Que la température joue un grand rôle dans la croissance des arbres, cela ne fait aucun doute. Bien plus, comme l'a montré Hustich (42, 43) à propos du *Pinus sylvestris*, il semble bien que le facteur dominant de la croissance n'est pas la précipitation, mais la température du milieu de l'été.

Ce point de vue semble admis par le plus grand nombre des chercheurs (35, 36). Il me semble tout à fait juste que Hare base sa corrélation sur les frontières des provinces thermiques proposées par Thornthwaite (123, 124, 125). Ces frontières seraient tirées des courbes de la température efficiente (*thermal efficiency* de Thornthwaite). Pour bien comprendre ce système, je ne puis mieux faire que de citer Villeneuve et Hare: "Au lieu d'employer seulement les valeurs de température et de précipitation pour déterminer les climats régionaux, Thornthwaite apporta deux nouveaux concepts: la température efficiente et l'efficacité de la précipitation. Il obtient la température efficiente en divisant la température moyenne mensuelle par l'évaporation, et l'efficacité de la précipitation, en divisant la précipitation par l'évaporation (Villeneuve 130)". "Annual potential evapotranspiration is the function used by Thornthwaite to establish the degree of thermal efficiency possessed by a climate. It is an accumulating logarithmic function of monthly mean temperatures, regarded as expressing thermal efficiency on the basis of a presumed analogy with the control of growth rates by temperature (Hare, 35)".

En appliquant les données de Thornthwaite à la péninsule Québec -Labrador, Hare constate effectivement le parallélisme entre les frontières des zones biologiques et les courbes de la température efficiente. Ceci permet de distinguer par exemple dans le nord du Québec la *taïga* ou parc subarctique, la *toundra forestière* et la *toundra*. Le concept de *zone hémiarctique* trouve là une parfaite justification.

Où le problème se complique le plus, c'est dans la terminologie à choisir. Comme je crois l'avoir suffisamment démontré, il se présente deux points de vue bien différents. L'on peut envisager une parcelle de végétation en fonction de l'habitat seulement: on remarque vers le 55° lat. N., par exemple, le parc clairsemé de *Picea*, que j'appelle la *taïga*, et Hare, *open boreal woodland*. A côté se trouve un autre habitat, le lac, dont la végétation se réduit à quelques éléments. Tout près, un autre habitat, la berge munie d'une pauvre florule. Il y a aussi le rocher dénudé, la tourbière et j'en passe. Cette forêt de conifères, ces eaux, cette berge, ce rocher dénudé, cette tourbière de la zone subarctique diffèrent de la forêt conifèrienne. du lac, de la berge, du

rocher dénudé et de la tourbière du 48° lat. N. dans la zone tempérée. En franchissant quelques degrés de latitude vers le sud on retrouve des habitats analogues, mais d'une gamme différente. Pour caractériser un lac d'une latitude donnée, faudrait-il faire intervenir la forêt qui l'entoure, comme si la forêt était le seul critère de la variation végétale d'une latitude à l'autre? Les diverses associations animales et végétales des différents habitats n'existent pas seulement en fonction de la forêt,—la communauté d'arbres,—mais en fonction d'un ensemble de facteurs biologiques et climatiques. D'où la nécessité de zones géographiques bien définies, qui permettront d'ailleurs de rapprocher les habitats climatiquement analogues des continents différents. De cette façon, en caractérisant par exemple une plante comme une "espèce aquatique subarctique" (au lieu d'une "espèce des lacs de la forêt clairsemée boréale"), on la place immédiatement sur un plan universel.

Les notions de *zones biologiques* et d'*habitats végétaux dominants* (spatialement dominants) sont donc deux notions différentes qui peuvent cheminer parallèlement et qui ont chacune leur utilité. Pour faciliter la comparaison, voici un tableau indiquant les zones biologiques de la péninsule Québec–Labrador, avec, en regard, leur habitat dominant, le nom de ces derniers dans les terminologies de Hustich et de Hare et les types climatiques correspondants définis par Villeneuve.

Zones d'après Rousseau	Habitat dominant d'après Rousseau	Habitat dominant d'après Hustich (44)	Habitat dominant d'après Hare (35)	Types climatiques de Villeneuve (130)
Arctique	Toundra	Tundra	Tundra	Toundra
Hémiarctique	Toundra forestière (Forest tundra)	Forest tundra	Forest tundra ecotone	Taïga
Subarctique	Taiga ou parc subarctique	Taiga	Open boreal woodland	
Tempérée	Forêt coniférienne tempérée	Southern spruce forest	Main boreal forest	Climat tempéré
	Forêt de bois mêlés	0	Boreal mixed forest ecotone	
	Forêt décidue ou forêt feuillue[11]	0	Great lakes St. Lawrence mixed forest[11]	

Dans la taïga, on distingue différents types dominants de forêts, qu'a bien caractérisés Hustich (44). Néanmoins ils ne sont pas aussi nombreux que dans la zone tempérée. De même que la flore s'accroît en espèces, depuis le haut arctique jusqu'à la limite sud de la zone tempérée, de même les types écologiques dominants semblent de plus en plus variés à mesure que l'on progresse vers l'équateur.

[11] *Les deux derniers termes de Rousseau et de Hare ne sont pas absolument parallèles.*

Fig. 3. Début du parc subarctique sur les îles du centre du lac Mistassini: végétation arborescente clairsemée, sol recouvert d'Ericacées, de *Betula glandulosa*, de Lichens (et surtout *Cladonia*). (Ph. Jacques Rousseau)

Fig. 4. Parc subarctique entre le lac Attikonak et la chute Hamilton; arbres très espacés, sol littéralement recouvert de *Cladonia*. A gauche, tourbière subarctique typique, à bandes parallèles causées par la solifluxion. (Ph. Jacques Rousseau)

Fig. 5. La zone hémiarctique, dans le voisinage de la base de Fort-Chimo. Les arbres sont restreints pour la plupart au voisinage des rivières. La plus grande partie du territoire est occupée par la toundra où les formations de *Cladonia* donnent l'impression que le sol est couvert de neige. (Ph. Jacques Rousseau)

Fig. 6. La zone hémiarctique, dans le voisinage de la base de Fort-Chimo. A gauche, parcelle de taïga (parc subarctique) typique. A droite, parcelle de toundra typique. Dans l'hémiarctique, on passe presque sans transition d'une

FIG. 7. La rivière George, dans la zone hémiarctique, par 55° 49′ 30″ lat. N. La formation d'arbres n'occupe que la vallée seulement. Parfois même, comme on le remarque à gauche, les parcelles de toundra se rendent jusqu'à la rivière ou presque. (Ph. Jacques Rousseau)

FIG. 8. Dans la zone hémiarctique. Le mont Pyramid sur la rivière George par 57° 29′ lat. N. La parcelle de taïga est restreinte à la base et, une quinzaine de mètres à peine au-dessus de la rivière, l'on passe à la toundra typique. (Ph. Jacques Rousseau)

FIG. 9. Dans la zone hémiarctique, une douzaine de kilomètres à l'ouest du lac Indian House, par 56° 19′ lat. N. Les parcelles arctiques sont telles qu'on ne voit pas un seul arbre à l'horizon parfois. (Ph. Jacques Rousseau)

FIG. 10. Au voisinage de Povungnituk, dans la zone arctique, la toundra typique: formation entièrement dépourvue d'arbres, fréquentée autrefois par le caribou arctique et habitée dans la zone littorale par les Esquimaux vivant surtout de la mer et de la chasse au renard blanc. (Ph. Jacques Rousseau)

FIG. 11. A la source de la rivière Kogaluk, dans la zone arctique. Toundra typique. (Ph. Jacques Rousseau)

Références

1. Abbe, E. C. Botanical results of the Grenfell–Forbes northern Labrador expedition, 1931. Rhodora, 38 : 102-161. 1936.
2. Abbe, E. C. Phytogeographical observations in northernmost Labrador. *In* Forbes, Alexander. Northernmost Labrador mapped from the air. Am. Geog. Soc. Spec. Pub. No. 22, New York. 1938.
3. Anonyme. Plants from Labrador. Roy. Botan. Gardens, Kew, Bull. Misc. Inform. pp. 76-88. 1907. (Etude des plantes de William MacGregor, récoltées en 1905.)
4. Ascherson, P. F. A. Nachtrag zur Flora von Labrador. Flora, 43 : 369-370. 1860.
5. Aubert de la Rüe, Edgar. Premiers résultats d'une traversée de la péninsule d'Ungava (Labrador canadien). Compt. rend. Soc. géol. France, 8 nov. : 271-272. 1948.
6. Aubert de la Rüe, Edgar. Quelques observations biogéographiques intéressant la péninsule d'Ungava (Labrador septentrional). Compt. rend. Soc. Biogéograph. 26 : 50-58. 1949.
7. Black, Robert F. Permafrost. Smithsonian Rept. 1950, pp. 273-301. 1951. (Reprint: Publication 4033.)
8. Braun, E. Lucy. Deciduous forests of Eastern North America. Blakiston, Toronto. 1950.
9. Butler, S. R. Labrador plants. Can. Nat. 5 (n.s.) : 350-353. 1870.
10. Cailleux, André et Taylor, Gérald. Etudes de cryopédologie. Expéditions polaires françaises, Missions Paul-Emile Victor, Expédition arctique, Section des Sciences naturelles, Paris. 1948.
11. Cain, Stanley A. The climax and its complexities. Am. Midland Naturalist, 21 : 146-181. 1939.
12. Clements, F. E. Nature and structure of the climax. J. Ecol. 24 : 252-284. 1936.
13. Coleman, A. P. La partie nord-est du Labrador et le Nouveau-Québec. Canada, Commission géol., Mém. 124, 1922. Appendice I: Plantes recueillies par le professeur A. P. Coleman dans son excursion du Labrador, pendant l'été de 1915 et identifiées par R. B. Thomson et Norma Ford. (Original en anglais.)
14. Delabarre, E. B. Report of the Brown-Harvard expedition to Nachwak, Labrador, in the year 1900. Bull. Geograph. Soc. Philadelphia, 2 : 65 et seq. 1901-03.
15. Delabarre, E. B. The Flora (of Labrador). Chap. 16. de Grenfell, Wilfred T. and others. Labrador, the country and people. The MacMillan Company, New York. 1909.
16. Dice, Lee R. The biotic provinces of North America. University of Michigan Press, Ann Arbor. 1943.
17. Doutt, Margaret T. Twin Island: an arctic outpost. Carnegie Magazine, 9 : 195-200. 1935.
18. Dutilly, Arthème et Lepage, Ernest. Coup d'œil sur la flore subarctique du Québec, de la baie James au lac Mistassini. Naturaliste can. 72 : 185-225, 266-288. 1945; 73 : 419-436. 1946; 74 : 43-60, 66-79, 177-189, 207-224, 250-273. 1947. Aussi tirage à part, Contrib. Arctic Inst. The Catholic University of America, Washington, D.C. No. 1, 1948.
19. Dutilly, Arthème et Lepage, Ernest. La traversée de l'Ungava en 1945. Naturaliste can. 77 : 136-181. 1950.
20. Dutilly, Arthème et Lepage, Ernest. La traversée de l'Ungava en 1945. Liste annotée des plantes vasculaires. Naturaliste can. 78 : 5-77. 1951.
21. Dutilly, Arthème et Lepage, Ernest. Exploration sommaire de la rivière Harricana. Naturaliste can. 78 : 253-284. 1951.
22. Farlow, W. G. List of algae collected at points in Cumberland Sound during the autumn of 1877. Bull U.S. Natl. Museum, No. 15. 1879. (Plantes récoltées par Turner.)
23. Fernald, M. L. A botanical expedition to Newfoundland and southern Labrador. Rhodora, 13 : 109-163. 1911.
24. Fernald, M. L. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts Sci. 15 (3) : 241-342. 1925.
25. Fernald, M. L. Recent discoveries in the Newfoundland Flora. Rhodora, 35 : 1-16; 47-63; 80-107; 120-140; 161-185; 203-223; 231-247; 265-283; 298-315; 327-346; 364-384; 395-403. 1933. Aussi Contrib. Gray Herbarium Harvard Univ. No. 105. 1934.

26. Fernald, M. L. and Sornborger, J. D. Some recent additions to the Labrador flora. Ottawa Naturalist, 13 : 89-107. 1899.

27. Flaherty, Robert. Two traverses across Ungava peninsula, Labrador. Geograph. Rev., pp. 116-132. Aug. 1918.

28. Fowler, James M. A. Arctic plants growing in New Brunswick with notes on their distribution. Proc. Roy. Soc. Can., IV, 5 : 189-205. 1887.

29. Gadbois, Pierre. De la baie d'Hudson à la baie d'Ungava. Actualité écon. (Montréal) 25 : 300-322. 1949.

30. Gardner, Gérard. Liste annotée des espèces de ptéridophytes, de phanérogames et d'algues récoltées sur la côte du Labrador, à la baie d'Hudson et dans le Manitoba nord, en 1930 et 1933. Bull Soc. botan. France, 84. 1937.

31. Gardner, Gérard. Liste des plantes récoltées sur la côte du Labrador et régions limitrophes. Bull. Soc. botan. France, V, 93. 1946.

32. Geographical Bureau, Ottawa. Mean annual temperature. Carte distribuée avec livraison d'Arctic, 2 (No. 1). 1949.

33. Halliday, W. E. D. A forest classification for Canada. Can. Dept. Mines Resources: Lands, Parks, Forests Branch, Dominion Forest Service, Bull. No. 89. 1937.

34. Hantzsch, Bernhard. Verzeichnis einer Anzahl in nordostlichsten Labrador gesammelter Pflanzenarten. Mitt. Ver. Erdk. Dresden, 1 (8) : 220-222. 1909. Traduction anglaise dans Can. Field Naturalist, 45 : 173-174. 1931. (Voir aussi Stein, Robert.)

35. Hare, F. Kenneth. Climate and zonal divisions of the boreal forest formation in Eastern Canada. Geograph. Rev. 40 (No. 4) : 615-635. 1950.

36. Hare, F. Kenneth. Some climatological problems of the arctic and sub-arctic. *in* Compendium of meteorology, pp. 952-964. 1951.

37. Harshberger, John. Phytogeographical survey of North America. Vol. 13 *de* Das Vegetation des Erde. Leipzig et New-York. 1911.

38. Hopkins, D. M. and Sigafoos, R. S. Frost action and vegetation patterns on Seward peninsula, Alaska, U.S.A. U.S. Geol. Survey Bull. 974-C. 1951.

39. Hubbard, Mrs. Leonidas, Jr. Labrador, from lake Melville to Ungava Bay. Bull. Am. Geograph. Soc. 38 : 529-539. 1906.

40. Hubbard, Mrs. Leonidas. A woman's way through unknown Labrador. Toronto (William Briggs). 1908. [Aussi éditions anglaise et américaine.]

41. Hustich, Ilmari. Notes on the coniferous forest and tree limit on the east coast of Newfoundland–Labrador, including a comparison between the coniferous forest limit on Labrador and in northern Europe. Acta geograph. 7 (No. 1). 1939.

42. Hustich, Ilmari. The Scotch pine in Northernmost Finland and its dependence on the climate in the last decade. Acta botan. fennica, No. 42. 1948.

43. Hustich, Ilmari. On the correlation between growth and the recent climatic fluctuation. *In* Glaciers and climate, *dedicated to* Hans Wilson Ahlmann. Geograf. Ann. 31 : 90-105. 1949.

44. Hustich, Ilmari. Phytogeographical regions of Labrador. Arctic, 2 : 36-42. 1949.

45. Hustich, Ilmari. On the forest geography of the Labrador Peninsula. A preliminary synthesis. Acta geograph. 10 (No. 2). 1949.

46. Hustich, Ilmari. Notes on the forests on the East coast of Hudson Bay and James Bay. Acta Geograph. 11 (No. 1). 1950.

46*a*. Hustich, Ilmari. Forest-botanical notes from Knob lake area in the interior of Labrador peninsula. Ann. Rept. Natl. Museum (Can.) for the fiscal year 1949-1950, pp. 166-217. 1951.

46*b*. Hustich, Ilmari. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. Acta geograph. 12 (No. 1). 1951.

47. Hustich, Ilmari and Pettersson, Bror. Notes on vascular plants of the East coast of Newfoundland–Labrador. I. Preliminary list of plants. Mem. Soc. Fauna et Flora Fennica, 19 : 192-200. 1944.

48. Hustich, Ilmari and Pettersson, Bror. Notes on vascular plants of the East coast of Newfoundland–Labrador. II. Notes by I. Hustich on the localities where the plant material was collected in 1937. Mem. Soc. Fauna et Flora Fennica, 20 : 24-46. 1945.

49. Jenness, J. L. Permafrost in Canada. Carte hors texte. Arctic, 2 (1). 1949.

50. KINDLE, E. M. Géographie et géologie du district du lac Melville, Presqu'île du Labrador. Canada, Commission géologique, Mém. 141. 1926. Aussi édition anglaise originale en 1924. La partie botanique est basée sur des herborisations de Wetmore. (Voir Wetmore (133)).

51. KUCYNIAK, JAMES. A bryophyte flora of interest on Lac des Cygnes mountain, Quebec. Bryologist, 50 : 327-350. 1947.

52. KUCYNIAK, JAMES. A list of Bryophytes collected in the George river district, Quebec. Bryologist, 52 : 173-187. 1949.

52*a*. KUCYNIAK, JAMES. Le genre *Splachnum* dans le Québec. Rev. bryol. et lich. 20 : 38-42. 1951.

53. LAWSON, GEORGE. Remarks on the flora of the northern shores of America, with tabulated observations made by Mr. F. F. Payne on the seasonal development of plants at Cape Prince of Wales, Hudson Strait, during 1886. Proc. Roy. Soc. Can., IV, 5 : 207-212. 1887.

54. LÉANDRI, J. Les tourbières et leur étude. Terre et Vie, 95 : 161-199. 1948.

54*a*. Le Gallo, C. Florule de la Vallée Matapédia. Notes phytogéographiques. Naturaliste can. 79: 142-170. 1952.

55. LEWIS, HARRISON F. An annotated list of vascular plants collected on the North shore of the Gulf of St. Lawrence, 1927-1930. Can. Field Naturalist, 45 : 129-135, 174-179, 199-204, 225-228. 1931; 46 : 12-18, 36-40, 64-66, 89-95. 1932.

56. LOW, A. P. Report on exploration in the Labrador peninsula along East Main, Koksoak, Hamilton, Manicuagan and portions of other rivers in 1892-93-94-95. Part 50. Ann. Rept. Geol. Survey Can. 8. 1896.

57. MACKAY, A. H. Labrador plants. (*Collected* by W. H. Frost on the Labrador coast north of Hamilton inlet, from the 25th of June to the 12th of August, 1901). Proc. Nova Scotian Inst. Sci. 10 : 507-508. 1903.

58. MACOUN, JAMES M. List of plants collected at Lake Mistassini, Rupert River and Rupert House, 1885. Appendix II *in* Low, A. P. Report of the Mistassini expedition 1884-85, pp. 36D-44D. Can. Geol. Survey, Montreal, 1885.

59. MACOUN, JAMES M. List of plants collected on the Rupert and Moose Rivers, along the shores of James bay and on the islands in James Bay during the summers of 1885 and 1887. Appendix I *in* Low, A. P. Report on explorations in James Bay and country east of Hudson Bay. Part J, Ann. Rept., Vol. III, Can. Geol. Nat. History Survey, pp. 63J-74J. 1887.

60. MACOUN, JAMES M. Catalogue of the plants reported by various travellers and others as growing on the coast of Labrador. *In* Packard, A. S. Labrador Coast, pp. 471-474. 1891.

61. MACOUN, JAMES M. List of plants known to occur on the coast and in the interior of the Labrador peninsula. Appendix VI *in* Low, A. P. Report on exploration in the Labrador peninsula along East Main, Koksoak, Hamilton, Manicuagan and portions of other rivers in 1892-93-94-95. Part 50. Ann. Rept. Geol. Survey Can., Vol. 8, pp. 353L-386L. 1896.

62. MACOUN, JAMES M. and MALTE, M. O. The flora of Canada. Can. Dept. Mines Geol. Survey, Museum Bull. No. 26 (Biol. Ser. No. 6). 1917.

63. MARIE-VICTORIN, F. Le dynamisme dans la flore du Québec. Contrib. Lab. Botan. Univ. Montréal, No. 13. 1929.

64. MARIE-VICTORIN, F. Quelques plantes nouvelles ou reliquales du bassin de la Baie des Chaleurs. Contrib. Lab. Botan. Univ. Montréal, No. 20. 1932.

65. MARIE-VICTORIN, F. Flore laurentienne. 1935. *Voir notamment* l'Esquisse générale de la flore laurentienne, pp. 19-78 de l'introduction.

66. MARIE-VICTORIN, F. Phytogeographical problems of Eastern America. Am. Midland Naturalist, 19 : 489-558. 1938. Aussi tirage-à-part, Contrib. Inst. Botan. Univ. Montréal, No. 30. 1938.

67. MARR, JOHN W. Ecology of the forest–tundra ecotone on the east coast of Hudson Bay. Ecol. Monographs, 18 : 117-144. 1948.

68. MEEN, V. BEN. Solving the riddle of Chubb Crater. Natl. Geog. Mag. 101 : 1–40. 1952.

69. MERRIAM, C. HART. The geographic distribution of life in North America with special reference to the mammalia. Annual report of the Board of Regents of the Smithsonian Institution showing the operations, expenditures and condition of Institution to July 1891, pp. 365-415. Washington 1893.

70. MERRIAM, C. HART. Life zones and crop zones. U.S. Dept. Agr., Div. Biol. Survey, Bull. No. 10. 1898.

71. MEYER, E. H. P. De plantis labradoricis libri tres. Leipzig. 1830.

72. Nordenskïold, Otto. Le monde polaire. Paris (Librairie Armand Colin). 1913.
73. Nordenskïold, Otto and Macking, Ludwig. The geography of the polar regions. Special pubs. Am. Geograph. Soc. No. 8. 1928.
74 Polunin, Nicholas. The Isle of Auks. London. 1932.
75. Polunin, Nicholas. Some notes on the vegetation of Akpatok island: Appendix III, Botany. Geog. J. 80 : 229-230. 1932.
76. Polunin, Nicholas The flora of Akpatok island, Hudson Strait. J. Botany, 72 : 197-204. 1934.
77. Polunin, Nicholas. The vegetation of Akpatok island. Part I. J. Ecol. 22 : 337-395. 1934. Part II. J. Ecol. 23 : 161-209. 1935. (Corrections of the determination of species.) J. Ecol. 25 : 570. 1937.
78. Polunin, Nicholas. Vascular plants from Mansel (Mansfield) island, N.W.T. Can. Field Naturalist, 52 : 5-9. 1938.
79. Polunin, Nicholas. Botany of the Canadian Eastern Arctic. I. Can., Natl. Museum Can., Bull. No. 92 (Biol. Ser. No. 24), Ottawa. 1940. II. Bull. No. 97 (Biol. Ser. No. 26). 1947. III. Bull. No. 104 (Biol. Ser. No. 32). 1948.
80. Polunin, Nicholas. Arctic unfolding. Hutchinson & Co., London. 1949.
81. Polunin, Nicholas. Report on botanical explorations in Arctic America, 1946-1948. Arctic, 2 (1) : 45-55. 1949.
81*a*. Pomerleau, René. Au sommet de l'Ungava. Rev. Univ. Laval, mai 1950.
81*b*. Porsild, A. E. A new *Antennaria* from northern Ungava. Can. Field Nat. 63 : 80-81. 1949.
82. Potter, David. Botanical evidence of post pleistocene marine connection between Hudson bay and the St. Lawrence Basin. Rhodora, 34 : 69-89; 101-112. 1932.
83. Potter, David. Plants collected in the southern region of James Bay. Rhodora, 36 : 274-284. 1934.
84. Ray, Louis L. Permafrost. Arctic, 4 : 196-203. 1951.
85. Raymond, Marcel. Esquisse phytogéographique du Québec. Mém. Jardin botan. Montréal, No. 5. 1950.
86. Raymond, Marcel. Les Cypéracées de l'île Anticosti: *Carex* et *Kobresia*. Can. J. Research, C, 28 : 406-444. 1950.
87. Raymond, Marcel. Histoire et distribution du *Carex Williamsii*. Naturaliste can. 77 : 222-227. 1950.
88. Raymond, Marcel. Sedges as material for phytogeographical studies. Mém. Jardin botan. Montréal, No. 20. 1951.
89. Rouleau, Ernest. Enumeratio plantarum vascularum Terrae-Novae. Contribs. Inst. Botan. Univ. Montréal, 64 : 61-85. 1949.
90. Rousseau, Jacques. Etudes floristiques sur la région de Matapédia (Québec). Musée Natl. Can. Bull. 66 : 1-25. 1931.
91. Rousseau, Jacques. Notes sur la flore de Saint-Urbain, comté de Charlevoix (Québec). Musée Natl. Can. Bull. 66 : 26-36. 1931.
92. Rousseau, Jacques. Contribution à l'étude du *Gentiana Victorinii*. Contrib. Lab. Botan. Univ. Montréal, No. 23. 1932.
93. Rousseau, Jacques. Les Astragalus du Québec et leurs alliés immédiats. Contrib. Lab. Botan. Univ. Montréal, No. 24. 1934.
94. Rousseau, Jacques. The part played by some tidal plants in the formation of clay rhizoconcretions. J. Sediment. Petrol. 4 : 60-64. 1934.
95. Rousseau, Jacques. La batture de l'île aux Grues et son importance économique. Vingt-cinquième et vingt-sixième rapports annuels de la Soc. de Québec pour la Protection des Plantes, 1932-34, pp. 82-86, 1934. [Aussi édition anglaise.]
96. Rousseau, Jacques. Le rôle de certaines plantes ripariennes dans la formation de concrétions argileuses. Naturaliste can. 62 : 99-105. 1935. Aussi Contrib. Lab. Botan. Univ. Montréal, 29 : 21-27. 1937.
97. Rousseau, Jacques. Les tourbières littorales: indice de la submersion de la côte sud-est de la Nouvelle-Ecosse. Naturaliste can. 64 : 197-206. 1937. Aussi Contrib. Lab. Botan. Univ. Montréal, 29 : 81-90. 1937.
98. Rousseau, Jacques. Notes floristiques sur l'est de la Nouvelle-Ecosse. Naturaliste can. 65 : 285-315; 317-335. 1938. Aussi Contrib. Inst. Botan. Univ. Montréal, 32 : 13-62. 1938.
99. Rousseau, Jacques. Additions à la flore de l'île d'Anticosti. Naturaliste can. 69 : 97-122. 1942. Aussi Contrib. Inst. Botan. Univ. Montréal, 44 : 11-36. 1942.

100. Rousseau, Jacques. Les rhizoconcrétions argileuses et les balles sablées. Naturaliste can. 69 : 213-221. 1942. Aussi Contrib. Inst. Botan. Univ. Montréal, 44 : 43-51. 1942.

101. Rousseau, Jacques. La forme naine du *Plantago juncoides* et autres espèces Naturaliste can. 69 : 234-239. 1942. Aussi Contrib. Inst. Botan. Univ. Montréal, 44 : 65-72. 1942.

102. Rousseau, Jacques. Le voyage d'André Michaux au lac Mistassini en 1792. Rev. Hist. Am. française, 2 : 390-423. 1948. Aussi tirage-à-part. Mém. Jardin botan. Montréal, No. 4. 1948.

103. Rousseau, Jacques. The vegetation and life zones of George river, Eastern Ungava, and the welfare of the natives. Arctic, 1 (No. 2) : 93-96. 1948.

104. Rousseau, Jacques. By canoe across the Ungava peninsula via the Kogaluk and Payne rivers. Arctic, 1 (No. 2) : 133-135. 1948.

105. Rousseau, Jacques. À travers l'Ungava. Actualité écon. 25 : 83-131. 1949. Aussi Mém. Jardin botan. Montréal, No. 4. 1949.

106. Rousseau, Jacques. La zone hémiarctique. Proc. and Trans. Roy. Soc. Can., 43 (Sér. 3) (app. F) : 246. 1949.

107. Rousseau, Jacques. Modifications de la surface de la toundra sous l'action d'agents climatiques. Rev. can. Géog. 3 : 43-51. 1949. Aussi Mém. Jardin botan. Montréal, No. 6. 1949.

108. Rousseau, Jacques. Cheminements botaniques à travers Anticosti. Can. J. Research, C, 28 : 225-272. 1950. Aussi Mém. Jardin Botan. Montréal, No. 12, 1950.

108*a*. Rousseau, Jacques. Le caribou et le renne dans le Québec arctique et hémiarctique. Rev. can. Géog. 4 : 60-89. 1950.

108*b*. Rousseau, Jacques. Notes sur quelques lichens antibiotiques de la province de Québec. Aspects écologiques et phytogéographiques. Rev. can. biol. 10 : 181-182. 1951.

108*c*. Rousseau, Jacques. De la baie d'Ungava aux Torngat. Notes sur la vie animale. Rapp. ann. Assoc. Prov. Qué. Protection poisson et gibier, 93 : 21-27. 1952. (Also English translation.)

109. Rousseau, Jacques. The value of botany as indicator of unglaciated areas. Pacific Sci. Congress (1949). Sous presse.

110. Rousseau, Jacques. Flora and vegetation in Quebec and Labrador. Arctic Encyclopedia. Sous presse.

111. Rousseau, Jacques et Bernard. Étude comparative de la température de l'estuaire du Saint-Laurent et des habitats voisins. Naturaliste can. 64 : 127-131. 1937. Aussi Contrib. Lab. Botan. Univ. Montréal, 29 : 65-69. 1937.

112. Rousseau, Jacques et Raymond, Marcel. *Betula Michauxii* in Northeastern America. Rhodora, 52 : 27-32. 1950.

112*a*. Rousseau, Jacques et Raymond, Marcel. Un *Agoseris* nouveau pour l'est de l'Amérique du nord. Nat. can. 78 : 353-360. 1951.

112*b*. Rousseau, Jacques, et Raymond, Marcel. Le *Gentiana tenella* Rottb. dans le Québec arctique. Nat. can. 79 : 76-80. 1952.

112*c*. Rousseau, Jacques, et Raymond, Marcel. Quelques entités nouvelles du nord du Québec. Nat. can. 79 : 81-84. 1952.

113. Saint-Cyr, Dominique-Napoléon. Rapport d'un voyage d'exploration sur les côtes du Labrador et les îles du golfe par M. Saint-Cyr. [Titre indiqué dans le sommaire seulement.] pp. 3-29 de Réponse à une adresse de l'Assemblée législative en date du 19 avril 1886 demandant copie du rapport d'un voyage fait au Labrador Canadien, en vertu d'un ordre en conseil, par M. Saint-Cyr, ancien député, conservateur du Musée de l'Instruction publique. Québec, 20 mai 1886. Aussi édition anglaise: Return to an address of the Legislative Assembly . . . April 19, 1886 (No. 17 B).

114. Saint-Cyr, Dominique-Napoléon. Liste des plantes récoltées par D. N. Saint-Cyr sur la côte Nord, depuis la baie Saint-Paul jusqu'à Ouatchechou et dans les îles de Mingan, d'Anticosti et de Grand Mécatina, pendant l'été de mil huit cent quatre-vingt-deux et le mois de juillet mil huit quatre-vingt-cinq, durant les loisirs de ses deux voyages dans le bas du fleuve et le golfe Saint-Laurent. [Titre du sommaire: Liste des plantes recueillies par M. Saint-Cyr sur la côte nord et les îles du golfe durant les étés 1882 et 1885] pp. 70-83 de Réponse à une adresse. . . [Pour titre complet, voir 113]. Aussi édition anglaise: List of plants gathered on the north shore, from St. Paul bay to Ouatchechou, and in the islands of Mingan, Anticosti, and Grand Mécatina, during the summer of 1882 and the month of July, 1885, during the leisure hours of his two trips to the lower St. Lawrence and the gulf.

115. Saint-Cyr, Dominique-Napoléon. Catalogue des plantes de la collection du Musée de l'Instruction publique récoltées par D. N. Saint-Cyr, jusqu'en mil huit cent quatre-vingt-cinq ou acquises par échange ou par achat. [Titre du sommaire: 7. Catalogue des plantes de la collection botanique du Musée de l'Instruction publique. 8. Catalogue des plantes cryptogames.] pp. 84-158 de Réponse à une adresse. . . [Pour citation complète voir 113]. Aussi édition anglaise: Catalogue of plants in the Museum of the Department of Public Instruction, gathered by D. N. Saint-Cyr, up to 1885, or acquired by exchange or purchase.

116. St. John, Harold. A botanical exploration of the North shore of the gulf of St. Lawrence, including an annotated list of the species of vascular plants. Can., Victoria Museum, Mem. No. 126. 1922. [L'auteur donne un excellent aperçu des explorations et travaux antérieurs.]

117. Sargent, C. S. Journal of André Michaux, 1787-1796, with an introduction and notes by Charles Sprague Sargent. Proc. Am. Phil. Soc. Vol. 26. 1888.

118. Schlechtendal, D. F. L. von. Ueber die Flora von Labrador. Linnaea, 10 : 76-114. 1836.

119. Scoggan, H. J. The flora of Bic and the Gaspé peninsula, Québec. Natl. Museum Can. Bull. No. 115 (Biol. Ser. No. 39). 1950.

120. Sigafoos, R. S. Soil instability in tundra vegetation. Ohio J. Sci. 51 : 281-298. 1951.

121. Stein, Robert. Bernhard Hantzsch's notes on Northeastern Labrador. Bull. Am. Geog. Soc. 41 : 566-575. 1909.

122. Tanner, V. Outlines of the geography, life and customs of Newfoundland–Labrador. Cambridge University Press, 2 Vols. 1947.

123. Thornthwaite, C. Warren. The climates of North America according to a new classification. Geograph. Rev. 21 : 633-655. 1931.

124. Thornthwaite, C. Warren. The climates of the earth. Geog. Rev. 23 : 433-440. 1933.

125. Thornthwaite, C. Warren. An approach toward a rational classification of climates. Geograph. Rev. 38 : 55-94. 1948.

126. Todd, W. E. Clyde. Ungava and the barren grounds. Carnegie Mag. 165-170. 1945.

127. Troll, Carl. Strukturböden, Solifluktion und Frostklimate der Erde. Sonderdruck aus der Geologischen Rundschau, Band 34. Heft 7-8, pp. 545-694. 1944.

128. Turner, Lucien M. The physical and zoological character of the Ungava district, Labrador. Trans. Roy. Soc. Can., IV, 5 : 79-83. 1887.

129. Turner, Lucien M. Ethnology of the Ungava district, Hudson bay territories. Smithsonian Institution, Eleventh Ann. Rept. Bur. Ethnol. pp. 167-350. 1894. [Renferme quelques notes botaniques.]

130. Villeneuve, G. Oscar. Aperçu climatique du Québec. Québec, Ministère des Terres et Forêts, Bull. No. 10. 1948.

131. Wallace, Dillon. The long Labrador trail. The Outing Pub. Co., New York. 1907.

132. Washburn, A. L. Patterned ground. Rev. can. Géograph. 4 (Nos. 3-4) : 5-59. 1950.

133. Wenner, Carl-Gosta. Pollen diagrams from Labrador. A contribution to the quaternary geology of Newfoundland–Labrador, with comparisons between North America and Europe. Geograf. Ann. (Stockholm). Aussi tirage-à-part. 1947.

134. Wetmore, R. H. Plants of the Hamilton Inlet and lake Melville region, Labrador. Rhodora, 25 : 4-12. 1923.

135. Wheeler, 2nd. E. P. Topographical notes on a journey across Labrador. Geograph. Rev. 28 : 475-481. 1938.

136. Woodworth, R. H. Interesting plants of Northern Labrador. Rhodora, 29 : 54-57. 1927.

137. Wynne-Edwards, V. C. Some factors in the isolation of rare alpine plants. Trans. Roy. Soc. Canada, V, 33 (Ser. 3) : 1-8. 1939.

THE COMPOSITION OF AIR IN TRUNKS OF SUGAR MAPLE IN RELATION TO DECAY[1]

By D. G. Thacker[2] and H. M. Good[3]

Abstract

The internal air of maple trunks was found to vary considerably in composition, particularly in decaying trees. In all cases carbon dioxide occurred in much larger, and oxygen in smaller amounts than in the atmosphere. Carbon dioxide content was highest in the summer and lowest in midwinter, oxygen varying reciprocally. Diurnal variations were also noted. Growth of maple rot fungi on malt agar was favored by carbon dioxide in concentrations found in living trees. In several cases, optimum concentrations were of the order of 10%, growth being approximately double that in carbon dioxide-free air. Oxygen had little effect within the range of concentrations occurring in trees. It is concluded that aeration is probably not an important factor in the development of decay, poor aeration tending to be stimulating rather than inhibiting.

Introduction

The fungi which cause heart rots are principally wound parasites disseminated by air-borne spores. These cause infection when they germinate on an open wound, such as a branch stub or fire scar, and invade the exposed wood. The parasite will, therefore, begin infection in a normal atmosphere but must continue development within a massive organ, the trunk, under very different conditions of aeration. In addition, infection of the living maple trunk causes the formation of large amounts of wound gum in the tissues and it has been suggested (14) that this reduces aeration in the wood and so may hinder the growth of decay organisms. It is, therefore, of considerable interest to know the composition of the air in tree trunks at various stages of decay and the effects of such air on the growth of heart rot fungi. While it should not, perhaps, be assumed that carbon dioxide, oxygen, and nitrogen, are the only gases present in trees, the present study deals with these gases only.

While the composition of air in fleshy plant organs has received considerable attention, relatively little work has been done on that within tree trunks. MacDougal and Working (12) analyzed the gases from eight species of trees in the American southwest, and Chase (4) studied seasonal variations in the composition of the internal air of five species in Minnesota. Marked variations occurred between different species and at different times of the year. Oxygen was consistently lower and carbon dioxide considerably higher than in the atmosphere. In these studies a very limited number of trees was tested and no consideration was given to the effects of decay.

Studies of the effects of carbon dioxide upon fungal growth have given various results. Several fungi, isolated from decaying fruit, were inhibited at

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concentrations of 10 to 20% (3). *Rhizoctonia solani* was reported to grow normally in 2% but not in 3.8% (2), whereas *Alternaria solani* showed inhibitions at 0.5% (10) and *Ophiobolus graminis* at levels above 0.25% (6). High concentrations of carbon dioxide gave various degrees of inhibition with a number of wood rot fungi (1). On the other hand concentrations up to 32% caused little if any inhibition of *Neurospora sitophila* (5) and stimulation of *Penicillium roqueforti* has been reported at concentrations of the order of 30% (8). *Fusarium culmorum* grew better in concentrations close to 4% carbon dioxide than in air (2). Collectively these reports suggest that fungi respond very differently to carbon dioxide and that some may be benefitted by concentrations well above the quantities essential for fungus growth (7).

In contrast to the wide variations in the carbon dioxide tolerance of fungi, most species seem to be ndifferent to substantial variations in oxygen tension. Oxygen had little effect on the growth of fruit decay fungi (3) and growth of *Neurospora* was not significantly retarded until the oxygen concentration fell below 0.05% (5). Less than 2% was required for normal development of *Penicillium roqueforti* (8) though inhibition of *Ophiobolus* occurred below 6% (6). *Alternaria* (10) grew well in air of only 2% oxygen. In a more precise physiological test of the effects of oxygen, *Polystictus versicolor* was found to be sensitive to oxygen fluctuations in a range of partial pressures below 10 mm. of mercury, but relatively insensitive to partial pressures from 15 to 745 mm. (15).

Materials and Methods

Air samples were withdrawn through a steel tap, driven and sealed into holes bored at breast height, Fig. 3. The tap is shown in Fig. 1. It consisted of a tapered steel shank $5\frac{3}{4}$ in. long and $\frac{1}{2}$ to $\frac{3}{8}$ in. in diameter. A heavy collar at the larger end provided a surface against which a block fitted while the tap was being driven into the tree, and a projection beyond the collar served for the attachment of a rubber tube connecting the tap with the extraction apparatus. Two plates, one threaded for two half inch bolts were used as shown in Fig. 1 for withdrawing the tap. A fine bore, of 1/64 in. diameter, ran through the tap and connected with eight inlet holes located at the inner end. This number of inlets into the tap was made lest some become plugged during the insertion of the tap into the trunk.

Before boring a hole, the surface of the bark was smoothed with a sharp chisel until a crack-free surface was obtained. A hole was then bored, of a diameter slightly less than that of the upper portion of the tapered tap. When the tap had been driven tightly into the tree, it was sealed into position and the smoothed area painted with a sealing compound made up of five parts of melted beeswax to one of tar lap cement. This compound proved very tough and tenacious. It was also used to seal all rubber–glass joints prior to the application of suction.

Gas was extracted by connecting a mercury-filled 25 ml. pipette to the tap, Fig. 2. The pipette was connected at the bottom to a mercury reservoir, the height of which could be varied. When all connections had been sealed,

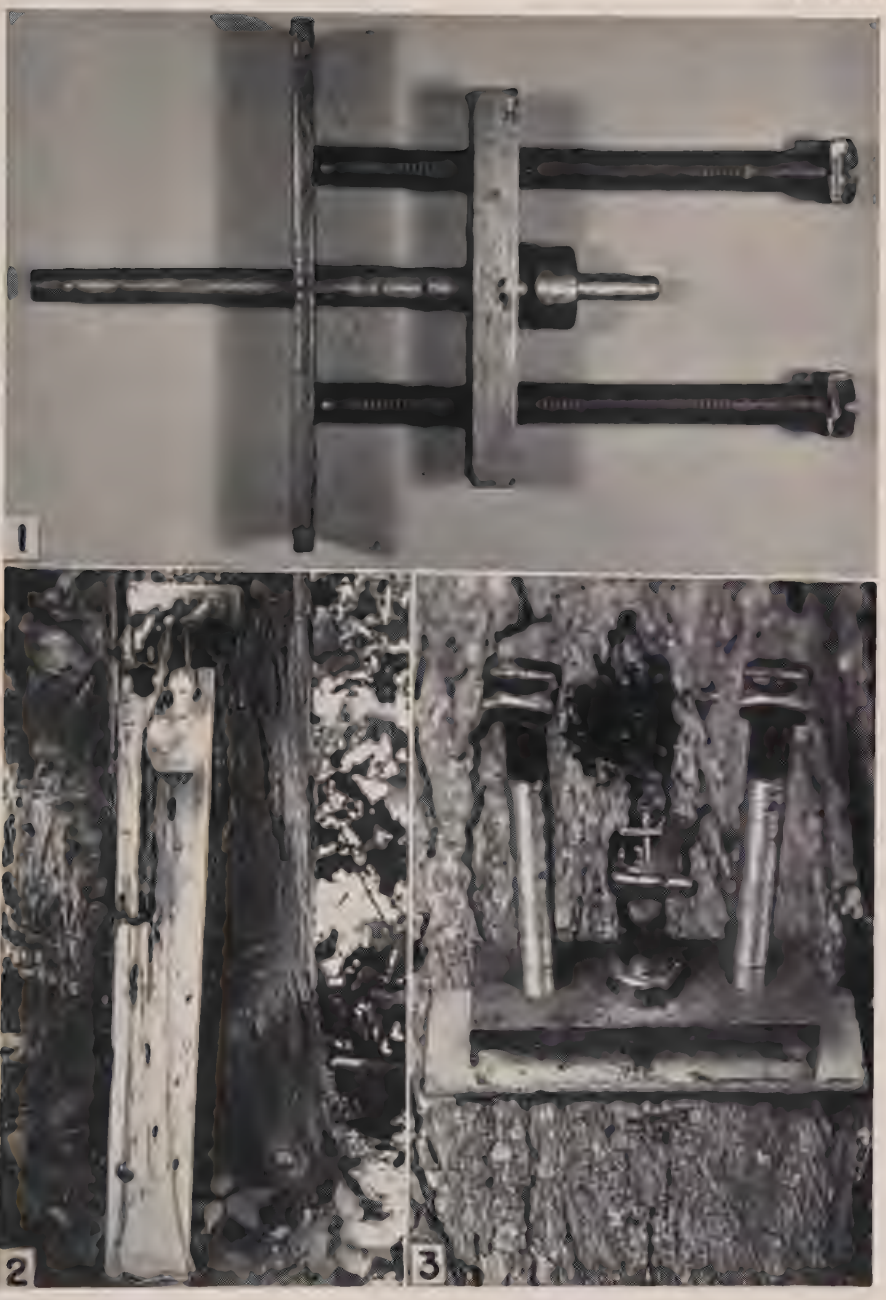

FIG. 1. Tap used for extracting air from trunks of maple trees shown with apparatus used for extracting it after sampling.

FIG. 2. Mercury filled pipette and reservoir used to draw air from the tree.

FIG. 3. The tap and withdrawal apparatus in position.

the reservoir was lowered, allowing the mercury to drain from the pipette. The resultant suction caused a flow of gas from the tree into the pipette. Two 25 ml. samples were withdrawn from each hole, the first being discarded to eliminate traces of atmospheric air in the borings. Tests showed that all but the first sample from a single hole gave substantially the same analysis if taken within a short period. The rates at which gas flowed from the trees varied considerably. In some cases the mercury fell readily. In others, over an hour was required to obtain a sample. The highest resistance to withdrawal was encountered in sound trees.

All the trees studied were in the region of the Queen's University Biological Station, Chaffey's Lock, Ont. Analyses for oxygen and carbon dioxide were made with a Fisher-Orsat portable gas analyzer. The burette of the analyzer was of 25 ml. capacity and was graduated in tenths of a milliliter. By reading to the nearest division, concentrations of gas as low as 0.4% could, therefore, be determined.

To determine the effect of carbon dioxide and oxygen on the growth of maple rot fungi, colony diameter increments were used as a measure of growth. The following fungi, isolated from decayed maple heartwood, were investigated: *Corticium vellereum* Ell. and Crag., *Ganoderma applanatum* (Pers.) Pat., *Polyporus hirsutus* Wulf ex Fr., *Pholiota adiposa* Fr., *Pholiota spectabilis* Fr., *Ustulina vulgaris* Tul., and *Hericium erinaceus* (Fr.) Pers. Pure cultures of these fungi were obtained from the Department of Agriculture, Division of Botany and Plant Pathology, Ottawa.

Colonies were grown on Petri plates of 2% malt agar at pH 5.5 and, when sufficiently advanced, small blocks about 2 mm. square were cut from the advancing edges and inverted upon fresh plates of malt agar. Four blocks of a fungus were placed on each plate. When the colonies were approximately 10 mm. across, their diameters were measured to the nearest millimeter and the Petri plates were placed in five-liter desiccators, a maximum of three plates in each.

To test the effects of carbon dioxide on growth, each desiccator was first evacuated to 65% of atmospheric pressure and after addition of the necessary volume of carbon dioxide, sufficient nitrogen was added to regain atmospheric pressure. In this way the concentration of oxygen in all the desiccators was maintained at approximately 13%. Zero concentrations of carbon dioxide were obtained by placing 10% potassium hydroxide in the bottom of the desiccator.

In those experiments where the concentration of oxygen was varied, nitrogen was also used to bring the partially evacuated desiccators back to atmospheric pressure. The initial concentration of carbon dioxide was never more than that of the atmosphere, about 0.03%, but this was increased appreciably during the experiments by the respiration of the fungi.

At the end of each experiment, a more accurate measure of the concentration was obtained by analyzing a sample of air from each desiccator. The desiccators were maintained under ordinary room conditions of light and tem-

perature, since Long and Harsch (11) found that light made the growth of wood-rotting fungi in culture more uniform and characteristic. The Petri plates were removed from the desiccators at the end of three days, and the diameters of the colonies were measured again, across the same diameters as had been measured previously. For each fungus, the average increase in diameter of four colonies was taken as the growth increment under each concentration of carbon dioxide and oxygen.

Results of Air Analyses

Comparison of Sound and Decayed Trees

In mid June and again in mid July, samples of air were withdrawn from the heartwood of 35 trees and analyzed. The percentages of carbon dioxide and oxygen in the June samples are given in Table I. In general, the composition of the samples was similar in July.

TABLE I

THE CARBON DIOXIDE AND OXYGEN CONTENT OF AIR EXTRACTED IN JUNE FROM SOUND AND DECAYED MAPLE HEARTWOOD

Tree No.	Diam., in.	Condition of heartwood	% Carbon dioxide	% Oxygen
20	9½	Sound	4.0	13.2
21	14	"	2.4	16.5
22	14	"	2.6	15.3
27	15½	"	4.8	13.6
29	11	"	1.9	17.7
30	12	"	2.4	14.4
31	12	"	3.6	12.4
34	14½	"	3.5	13.5
35	13	"	2.6	13.5
1	8	Discolored but firm	2.8	16.6
2	9	"	2.8	17.2
3	10	"	4.0	13.2
6	10	"	3.6	15.2
13	7	"	4.4	17.7
4	7½	Very soft and rotten	9.9	10.9
5	9½	"	3.7	16.5
7	8½	"	1.6	19.2
8	6½	"	4.0	16.4
9	7	"	5.2	3.2
10	9¾	"	14.8	4.4
11	5½	"	1.6	18.9
12	8	"	9.2	0.8
14	5½	"	6.6	13.6
15	11½	"	7.6	2.0
16	7½	"	8.0	1.2
17	7½	"	7.6	2.4
18	10	"	8.0	2.0
19	6	"	2.4	16.5
23	8	"	3.2	14.1
25	5	"	6.5	7.3
26	16	"	4.2	14.1
28	11	"	14.0	3.6
32	10½	"	11.8	8.5
33	12	"	16.9	3.2

In the heartwood of all the trees, the concentration of carbon dioxide was considerably higher than in the atmosphere. Oxygen tension was always less than atmospheric. A wide variation occurred in the amounts of these gases in different trees, carbon dioxide content ranging from 1.6% to 16.9% and oxygen from 0.8% to 19.2%. However, a grouping of the trees into the three classes of Table I shows that carbon dioxide and oxygen varied relatively little in sound trees or in those with discolored but firm centers. Large variations occurred in the trees with soft, punky heartwood. This is to be expected, since the wood-destroying fungi and the cells of the tree would utilize oxygen and produce carbon dioxide, but when the wood becomes punky, large wounds, cracks, or insect borings in the trunk might bring the center into direct contact with the external air.

Diurnal Variations

Diurnal fluctuations in the composition of the internal air were investigated. Samples were withdrawn from the heartwood of five sound and five decayed trees at different hours of the day and night for periods of several days. Since only one tap was available, the trees could not be done simultaneously. Temperature and weather conditions were noted at each extraction. The very considerable mass of data accumulated in this study has been recorded (16) and need not be repeated here. Only two records of diurnal variation of carbon dioxide are, therefore, given in Fig. 4. Similar, though occasionally more erratic, fluctuations took place in the other trees studied.

Both trees represented in Fig. 4 showed a definite diurnal fluctuation in carbon dioxide content, the variation being of the order of 2%. In sound trees the lowest concentrations of the gas occurred in the evening and the highest in

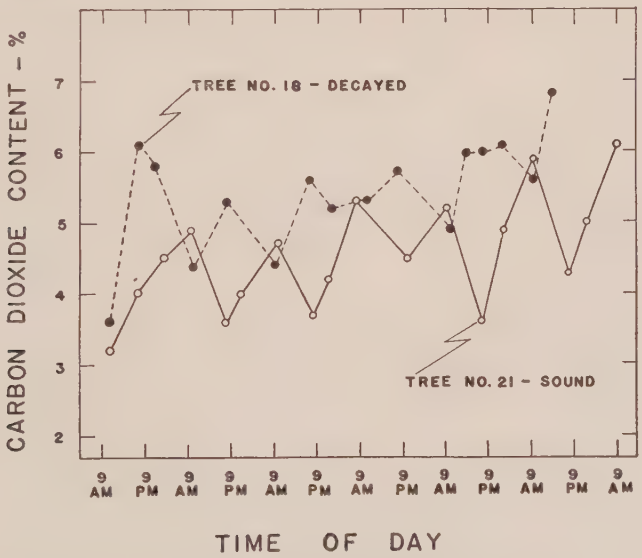

FIG. 4. Diurnal fluctuations in the carbon dioxide content of sound and decayed heartwood of sugar maple.

the morning. In seriously decayed trees the trend was reversed. In both types of trees oxygen fluctuated inversely to carbon dioxide. It has been shown (9) that parenchyma cells of maple wood may remain alive for more than half a century. If the carbon dioxide produced by the respiration of these cells can be transported to the leaves in the transpiration stream the diurnal fluctuations in sound wood are explainable. These factors cannot contribute to an explanation of the variations in decaying trees.

Comparison of Air from Central and Peripheral Regions of the Trunk

The report of Chase (4), that carbon dioxide was more abundant in heartwood than in sapwood, was checked by extracting gas from the centers of tree trunks and from depths of 2 in. in the trunks. Results of the tests on 27 trees, made during June, are given in Table II.

TABLE II

THE CARBON DIOXIDE AND OXYGEN CONTENT OF AIR EXTRACTED FROM 2 IN. INSIDE THE CAMBIUM AND FROM THE CENTERS OF SOUND AND DECAYED MAPLE TREES

Tree No.	Diam., in.	Condition of heartwood	% Carbon dioxide		% Oxygen	
			2 in. depth	Center	2 in. depth	Center
3	10	Sound	3.2	4.0	17.0	13.2
20	9½	"	3.6	4.0	11.5	13.2
21	14	"	1.2	2.4	17.1	16.5
22	14	"	2.4	2.6	15.6	15.3
29	11	"	1.9	2.7	17.7	16.8
30	12	"	2.0	2.5	14.0	13.8
31	12	"	4.8	4.8	13.2	10.9
34	14½	"	2.0	3.6	17.5	13.2
35	13	"	4.0	6.6	16.0	11.6
Average for sound heartwood			2.8	3.7	15.5	13.8
1	8	Decayed	4.2	2.8	12.6	16.6
2	9	"	2.6	2.8	19.2	17.2
4	7½	"	5.9	9.9	14.5	10.9
5	9½	"	2.5	3.7	17.3	16.5
6	10	"	2.2	3.6	17.3	15.2
7	8½	"	2.0	1.6	16.0	19.2
10	9¾	"	3.8	14.8	15.3	4.4
12	8	"	3.2	9.2	16.4	0.8
13	7	"	1.6	4.4	17.3	17.7
15	11½	"	2.1	7.6	16.1	2.0
17	7½	"	3.6	7.6	16.8	2.4
18	10	"	2.9	8.0	15.9	2.0
19	6	"	2.4	2.4	15.2	16.5
23	8	"	1.5	3.2	17.0	14.1
26	16	"	4.2	5.4	14.1	15.7
28	11	"	1.5	14.0	16.2	3.6
32	10½	"	3.6	11.8	16.1	9.4
33	12	"	2.0	17.7	16.8	2.4
Average for decayed heartwood			2.9	7.3	16.1	10.4

TABLE III

SEASONAL FLUCTUATIONS IN CARBON DIOXIDE** AND OXYGEN** CONTENT OF AIR EXTRACTED FROM MAPLE TREES

Tree No.	Diam., in.	Condition of heartwood	June	July	September	October	November	January
21	14	Sound	2.4/16.5	3.3/14.6	2.0/15.5	6.1/16.0	Sap*	—
22	14	"	2.6/15.3	4.4/12.9	4.5/12.8	4.2/15.3	Sap*	1.2/16.4
35	13	"	2.6/13.5	6.5/12.5	4.8/14.9	7.5/14.0	Sap*	2.5/27.3
31	12	"	3.6/12.4	6.5/2.9	4.0/12.9	7.9/9.0	Sap*	—
3	10	Discolored but firm	4.0/13.2	7.3/1.2	8.2/1.6	4.5/7.3	—	—
14	5½	Very soft and rotten	6.6/13.6	6.0/16.2	4.0/17.0	2.8/16.8	1.2/17.7	0.4/20.6
16	7½	"	8.0/1.2	4.6/13.8	5.2/12.9	5.2/11.3	4.4/9.3	2.8/9.2
9	7	"	5.2/3.2	7.0/11.3	12.1/7.3	9.3/9.3	4.5/13.1	—
12	8	"	9.2/0.8	13.7/3.6	12.0/3.6	8.5/4.9	—	—
32	10½	"	11.8/8.5	10.9/5.7	—	8.1/8.9	—	—
33	12	"	16.9/3.2	17.0/1.2	6.8/13.9	—	—	—

** Prolonged extraction gave largely sap with insufficient air for analysis.*

*** Concentrations of oxygen and carbon dioxide are given together in the form: % carbon dioxide/% oxygen.*

Air extracted from the centers of nine sound trees averaged 3.7% carbon dioxide and 13.8% oxygen while that from regions about 2 in. inside the cambium averaged 2.8% carbon dioxide and 15.5% oxygen. Extractions from 18 decayed trees showed the air from a 2 in. depth to average 2.9% carbon dioxide and 16.1% oxygen, while that from the centers averaged 7.3% carbon dioxide and 10.4% oxygen. All shallow holes were entirely in sound wood and the similarity of the air extracted from the outer regions of decaying trees and sound trees indicates that there is little lateral diffusion of gases within the tree.

Seasonal Variations in Composition

Samples of air were withdrawn from the heartwood of 11 trees at intervals throughout the summer, autumn, and early winter and analyzed for carbon dioxide and oxygen. The results of these analyses are listed in Table III.

The difficulties of obtaining samples in November and January made it necessary to reduce the number of trees examined during these months to seven and four respectively. While final conclusions cannot be based upon such a small number of trees, it appears from Table III that, in sound trees, the concentration of carbon dioxide reaches a maximum sometime after June 15, remains at a fairly high level throughout the summer and early autumn and decreases markedly during the winter. The concentration of oxygen follows an opposite trend.

Results of Culture Experiments

Effects of Carbon Dioxide on Growth

Growth of the fungi was measured in concentrations of carbon dioxide ranging from zero to 35%. Fig. 5 shows the response of these fungi to carbon dioxide tension. At least two separate tests were conducted for each organism.

All fungi showed considerable growth even when the free carbon dioxide was absorbed by potassium hydroxide. However, the growth was greatly increased in atmospheric concentrations plus the full amount produced by the respiration of the fungi. Although the gas analyzer was not suitable for measuring such low concentrations accurately, these ranged from approximately 0.4 to 0.8%.

In no case did carbon dioxide in moderate amounts have an inhibiting effect. Of the six fungi tested, *Pholiota spectabilis* and *Pholiota adiposa* appeared to be relatively insensitive to carbon dioxide tension. The remaining four fungi all showed a marked increase in growth with increased carbon dioxide until a slight inhibition set in at concentrations above 10%. The optimum concentration for all appeared to be between 5 and 10%. Concentrations of 15 to 20% caused inhibition in all cases, but growth was still appreciable even at 35%. Maple heart rot fungi, therefore, appear to be stimulated rather than inhibited in growth by the concentrations of carbon dioxide found in maple trees.

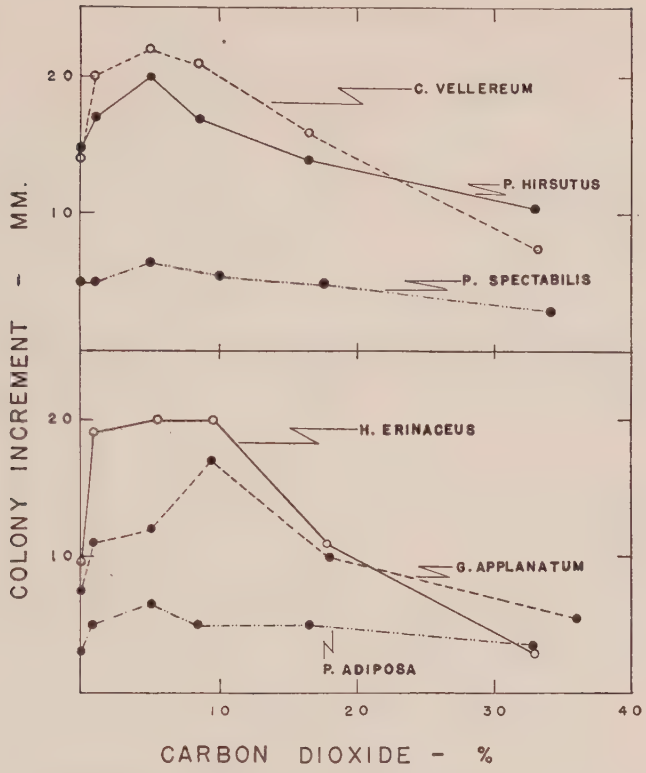

FIG. 5. The effects of carbon dioxide on growth in culture of six wood rot fungi.

Effect of Oxygen upon Growth

Several of the fungi were exposed to concentrations of oxygen ranging from 0.8 to 35%. Representative results are given in Fig. 6. Growth of all fungi was good at both 0.8 and 35% oxygen. Considerable variation occurred with different fungi but, in general, growth tended to increase slightly with increase of oxygen up to 10%, and decrease slightly or remain at a fairly steady level at higher oxygen tensions.

In only one case, *P. hirsutus*, was there evidence that the concentrations of oxygen found within maples might play a significant role in growth and even in this case the effect was not marked.

Discussion

No evidence was obtained that the dark, firm, wound gum wood, regularly formed during the early stages of maple decay (9), had lower oxygen or higher carbon dioxide content than normal wood. Indeed, it was only in the advanced stages of decay, when the centers of the trees had become punky, that high carbon dioxide concentrations were encountered. There is, therefore, no

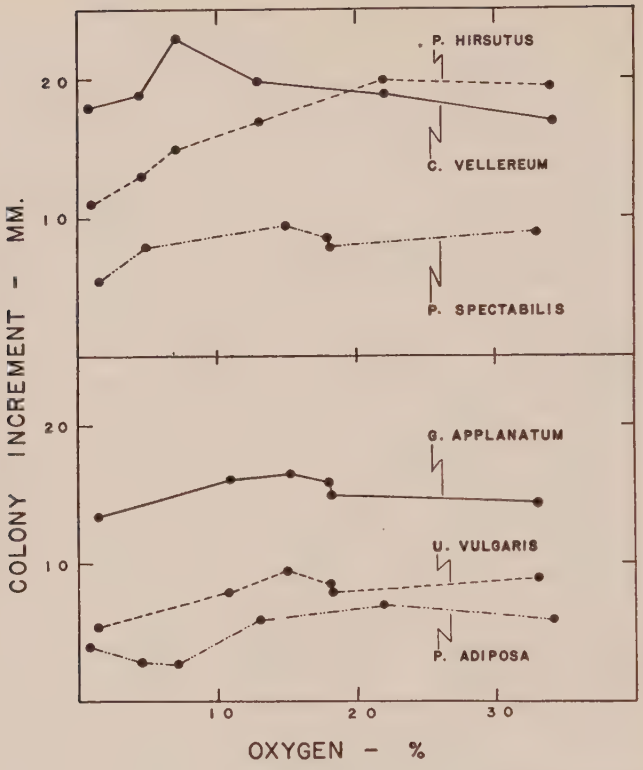

FIG. 6. The effects of oxygen on growth in culture of six wood rot fungi.

evidence that wound gum affects the air supply in the wood and any protection it affords the wood must be due to properties other than those influencing aeration.

Concentrations of carbon dioxide and oxygen in the tree were found to vary considerably with extent of decay and time of year. However, cultural evidence has been obtained that neither the highest concentration of carbon dioxide nor the lowest of oxygen found in the trees would cause marked inhibition of rot organisms and, until a method is devised for studying growth of decay organisms in living wood, it seems justifiable to conclude that the composition of air commonly found in maple trunks during the growing season is very nearly optimal for fungus development.

The stimulation of growth in culture by carbon dioxide was not a result of a modification of the pH of the medium, which was substantially unchanged by the concentrations of carbon dioxide tested. It would appear, therefore, that the carbon dioxide may be fulfilling a nutritive role, entering into the carbon metabolism of the fungus. In this connection an interesting review has recently been made available (13). This review reports that increased supply of carbon dioxide gave increased weight of mycelium and increased protein content in cultures of *Aspergillus flavus* and *Aspergillus oryzae*.

A further effect that carbon dioxide may have on decay of trees has been suggested by work done in association with the study reported here (16). The wound gum or stain area, which appears to be an invariable preliminary to decay of living maple, is alkaline when extracted with water. Decay fungi do not grow well in alkaline media. However, alkaline extracts of stained maple wood proved to be poorly buffered against carbon dioxide and this gas in the tree may be important as a modifier of the reaction. Details of this study will be provided in a later communication.

While all the effects of aeration on decay are still not understood, the data presented suggest that the idea of inhibition of decay fungi by "poor" aeration cannot at present be entertained, aeration in the tree appearing nearly optimal for decay. The effects of carbon dioxide and oxygen on metabolism of decay fungi should, however, be given further and more precise biochemical study.

References

1. Bavendamm, W. Neue Untersuchungen über die Lebensbedingungen holzzerstörender Pilze. I. Mitteilung: Gasversuche. Zentr. Bakt. Parasitenk. Abt. II, 75 : 426–452. 1928.
2. Braun, H. Untersuchungen über den Einfluss von Kohlensäure und Sauerstoff auf Keimung und Pflanzgutwert der Kartoffelknolle. Arb. biol. Reichsanstalt, Land-u. Forstw. Berlin-Dahlem, 19(1) : 18–93. 1931.
3. Brown, W. On the germination and growth of fungi at various temperatures and in various concentrations of oxygen and carbon dioxide. Ann. Botany, 36 : 257–283. 1922.
4. Chase, W. W. The composition, quantity and physiological significance of gases in tree stems. Univ. Minn. Agr. Expt. Sta. Tech. Bull. 99. 1934.
5. Denny, F. E. Oxygen requirements of *Neurospora sitophila* for formation of perithecia and growth of mycelium. Contribs. Boyce Thompson Inst. 5 : 95–102. 1933.
6. Fellows, H. The influence of oxygen and carbon dioxide on the growth of *Ophiobolus graminis* in pure culture. J. Agr. Research, 37 : 349–355. 1928.
7. Foster, J. W. Chemical activities of fungi. Academic Press Inc., New York. 1949.
8. Golding, N. S. The gas requirements of molds. Parts II and III. J. Dairy Sci. 23 : 879–890; 891–898. 1940.
9. Good, H. M. and Nelson, C. D. A histological study of sugar maple decayed by *Polyporus glomeratus* Peck. Can. J. Botany, 29 : 215–223. 1951.
10. Klaus, H. Untersuchungen über *Aternaria solani* Jones et Grout insbesondere über seine Pathogenitat an Kartoffelknollen in Abhängigkeit von den Autssenfaktoren. Phytopath. Z. 13 : 126–195. 1941.
11. Long, W. H. and Harsch, R. M. Pure cultures of wood rotting fungi on artificial media. J. Agr. Research, 12 : 33–82. 1935.
12. MacDougal, D. T. and Working, E. B. The pneumatic systems of plants, especially trees. Carnegie Inst. Wash. Pub. No. 441. 1933.
13. Pontovich, V. E. Utilization of CO_2 in synthetic processes of heterotrophic organisms. Izvestia Akad. Nauk SSSR, Biol. Ser. No. 5, pp. 120-135. 1951. (Review prepared by Dr. G. Krotkov.)
14. Rhoads, A. S. The black zone formed by wood-destroying fungi. N.Y. State Coll. Forestry, Tech. Pub. No. 8. 1917.
15. Scheffer, T. C. and Livingston, B. E. Relation of oxygen pressure and temperature to growth and carbon dioxide production in the fungus *Polystictus versicolor*. Am. J. Botany, 24 : 109-119. 1937.
16. Thacker, D. G. Investigations of heart rots of sugar maple. M.A. Thesis, Queen's University. 1951.

PHLORETIN: AN ANTIBACTERIAL SUBSTANCE OBTAINED FROM APPLE LEAVES[1]

By Russell E. MacDonald[2] and Charles J. Bishop[3]

Abstract

A crystalline antibacterial substance isolated from apple leaves has been identified as phloretin. It has been shown to inhibit the growth of a number of Gram-positive and Gram-negative bacteria. The activity of the compound is bacteriostatic in nature and is shown in concentrations as low as 30 p.p.m. Its antibacterial action may be related to inhibition of the uptake of phosphorus by the bacterial cell.

Introduction

During a survey of various higher plants for the presence of antibacterial substances, Bishop and MacDonald (2) found that alcohol, ether, and acetone extracts of leaves of apple, *Pyrus Malus* L. possessed a substance that exhibited antibiotic activity against *Staphylococcus aureus*. Further investigation of these extracts (3) has led to the isolation of a white crystalline compound which has been identified as phloretin (ω-p-hydroxyphenylpropiophenone), the aglucone of the glucoside phloridzin. According to Gortner (7), this glucoside has been found in the leaves, shoots, roots, and seeds of apple, cherry, pear, and certain other members of the Rosaceae, and its isolation has been previously reported.

Phloridzin has been employed commonly in the past to produce artificial glucosuria in experimental animals and in man. Phloretin has been found to display similar physiological activity. The effect of phloridzin on bacterial fermentation has been reported by Califano (4) and Wright (10). While both workers found that phloridzin inhibited the bacterial fermentation of sugars, they concluded that its activity was due to inhibition of the phosphate conversion of the sugar, thus rendering it unusable by the bacteria, and not to any direct effect on the organisms. The action of phloretin, however, was not tested.

Bioassay

Since phloretin is insoluble in water, the usual methods of assay could not be used. Tests showed it to be readily soluble in propylene glycol, and when it was dissolved in one milliliter of this solvent and added to 19 ml. of nutrient agar, concentrations of phloretin up to 2000 p.p.m. could be obtained with no visible precipitation in the media. No higher concentrations were tried. At this dilution controls showed that propylene glycol did not inhibit the growth of the test organisms.

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Contribution from Biological Laboratories, Acadia University, Wolfville, N.S. This project received financial support from the National Research Council of Canada and the Nova Scotia Research Foundation.

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TABLE I

THE ANTIBACTERIAL ACTIVITY OF PHLORETIN

Organism	Minimum inhibitory concentration, p.p.m.	Organism	Minimum inhibitory concentration, p.p.m.
Gram-positive organisms		Gram-negative organisms	
Bacillus cereus	30	*Aerobacter aerogenes**	500
*Bacillus megatherium**	500	*Aerobacter aerogenes**	500
*Bacillus megatherium**	30	*Alcaligenes viscosus*	1000
Bacillus mycoides	100	*Escherichia coli* ATCC 9637	100
Bacillus subtilis	30	*Escherichia coli*	500
Corynebacterium pseudodiphthericum	30	*Neisseria catarrhalis* ATCC 7900	50
Diplococcus pneumonia ATCC 6301	500	*Proteus vulgaris*	200
*Mycobacterium phlei***	<500	*Pseudomonas aeruginosa**	Inactive
*Sarcina lutea**	30	*Pseudomonas aeruginosa**	Inactive
*Sarcina lutea**	50	*Serratia marcescens*	1000
Staphylococcus aureus 209P	30	*Xanthomonas pruni***	<200
Staphylococcus aureus	50	Fungi	
Streptococcus faecalis ATCC 9790**	<500	*Aspergillus niger*	Inactive
		Penicillin sp.	Inactive

* *Different strains of the same organism.*
** *Tested by the cylinder plate method.*

The bacteria shown in Table I were tested using this method. Those marked with an asterisk were tested by the cylinder plate method of Heatley (8) and therefore the minimum inhibitory concentration could not be determined accurately.

The effect of pH on the activity of phloretin was determined using the cylinder plate method. Nutrient agar was adjusted to pH's varying from 6.0 to 8.0, poured into Petri dishes, and, when hard, seeded with *S. aureus*. A 1000 p.p.m. dilution of phloretin was tested in all cases. Table II shows that the activity of phloretin increased with an increase in the H-ion concentration.

TABLE II

THE EFFECT OF pH ON THE ANTIBACTERIAL ACTIVITY OF PHLORETIN

(Concentration of 1000 p.p.m. in acetone)

pH of agar	Activity (Av. zone of inhibition in mm.)
6.0	22.1
6.4	21.9
6.8	19.8
7.2	18.0
7.6	18.4
8.0	16.0

The bacteriostatic activity of phloretin was determined by using the "loop" method of Asheshov and Heagy (1) to count the number of viable bacteria at varying time intervals in a broth culture saturated* with phloretin. It was found that after a very slight initial increase in the number of bacteria the count remained constant for at least 48 hr.

The antibacterial action of phloretin was not inhibited by ascorbic acid, albumin, or lecithin, or by autoclaving in nutrient broth for 20 min. at 15 lb. pressure. It was reduced considerably by 1% whole blood. Phloretin obtained by hydrolysis of phloridzin with normal hydrochloric acid showed the same degree of activity as did that prepared from leaf extracts. The glucoside phloridzin showed no antibacterial activity.

Discussion

Although phloretin is active against both Gram-positive and Gram-negative bacteria, it seems to be more effective against Gram-positive organisms. Cavallito and Bailey (5) suggest that there is a relationship between the water solubility of nonionic antibacterials and their specificity towards bacteria, the water soluble ones being generally active against both Gram-positive and Gram-negative organisms, while the water insoluble ones are more active against Gram-positive bacteria. The results of the present experiments appear to bear out this observation.

The inactivity of the glucoside phloridzin indicates that the antibacterial activity of phloretin may be due to the group to which the glucose is attached. Shapiro (9) points out that the inhibitory action of phloridzin on glucose absorption in the kidney is exerted principally on oxidations with which phosphorylation of adenylic acid is coupled. It therefore seems probable that the effect of phloretin is due to a related inhibitory mechanism by which the uptake of phosphorus by the bacterial cell is prevented. A mode of action very similar to this is thought to be exerted by gramicidin (6).

Owing to its physiological action on glucose metabolism it is not likely that phloretin as such will be of much value therapeutically. However, its abundance in apple leaves (2.4% of dry weight (3)) makes them an economical source of the compound, and further work may prove it to have other uses, perhaps against certain plant pathogens.

Acknowledgments

The authors are indebted to E. G. Bligh for assistance in the isolation of phloretin, and to D. Chisholm for determining its solubility in cold water.

* *The solubility of phloretin in cold water was determined to be approximately 13 p.p.m.*

References

1. Asheshov, I. N. and Heagy, F. C. A 'loop' method for counting viable bacteria or bacteriophage. Can. J. Med. Sci. 29 : 1–4. 1951.
2. Bishop, C. J. and Macdonald, R. E. A survey of higher plants for antibacterial substances. Can. J. Botany, 29 : 260–269. 1951.
3. Bligh, E. G. An antibiotic principle from apple leaves. I. Isolation. II. Properties. Master thesis, Acadia University. 1951.
4. Califano, L. Inhibition by phloridzin of the fermentation of sugar by *E. coli*. Biochem. Z. 271 : 123–126. 1934.
5. Cavallito, C. J. and Bailey, J. H. An antibacterial principle from *Centaurea maculosa*. J. Bact. 57 : 207–212. 1949.
6. Dubos, R. J. *In* Antibiotics *edited by* G. W. Irving, and H. T. Herrick. Chemical Publishing Co. Inc., Brooklyn. 1941. p. 139.
7. Gortner, R. A. Outlines of biochemistry. John Wiley & Sons, Inc., New York. 1929.
8. Heatley, N. G. A method for the assay of penicillin. Biochem. J. 38 : 61–65. 1944.
9. Shapiro, B. The mechanism of phloridzin glucosuria. Biochem. J. 41 : 151–154. 1947.
10. Wright, H. D. The effect of iodoacetic acid, fluoride, phloridzin and phenol on bacterial fermentation. A further consideration of the fermentation of disaccharides. J. Path. Bact. 45 : 117–129. 1937.

ECOLOGICAL STUDY OF THE PEAT BOGS OF EASTERN NORTH AMERICA

I. STRUCTURE AND EVOLUTION OF VEGETATION[1]

By Pierre Dansereau[2] and Fernando Segadas-Vianna[3]

Abstract

It is attempted to clearly distinguish between bogs on the one hand and swamps and marshes on the other. The principal elements and factors are listed in Eastern North America where bogs are frequent. This first paper attempts a general outline of the dynamics of bog vegetation in this region and describes the structures of the communities involved. The biotope is considered the smallest piece in the association mosaic and its physical and biological aspects are emphasized. Two recent systems (Küchler's and Dansereau's) are applied to individualize the most important and widespread synecological units. Further studies involving climatic relationships on a geographical scale and phytosociological measurements at the quadrat level will permit a refocusing of some of the phenomena which are described and interpreted here.

In Eastern North America, bogs are frequent throughout the Wisconsin-glaciated territory and occur well beyond it to the south. They are, however, most common within the limits of the Canadian (or spruce-fir) forest region. Bog formations are therefore present in several major phytogeographic areas: the deciduous forest (including all nine segregates described by Braun (7,8)), the tall-grass prairie, the Canadian forest, and the taïga (or Hudsonian lichen woodland).

They present a number of interesting ecological and phytogeographic problems: (1) relation to regional vegetation, (2) mode of formation and effect on landscape, (3) evolution of vegetation, (4) composition and structure of communities. These aspects of bog study have been present in the senior author's mind in the course of field work in the years 1940-1945 and more especially during 1947 and 1948 when a more detailed investigation was made possible through grants from the National Research Council of Canada. The results of our field work will be presented in a series of papers. This first contribution will attempt a definition of terms, an outline of problems in dynamics, and the preliminary description of some key associations.

Bogs and Swamps: A Definition of Terms

The word *bog* is used, in ecological literature, in many different senses. It sometimes includes marshes and swamps as well as true bogs. Those who have used the term have emphasized various characteristics: physical, chemical, or vegetational. Schimper (45), Warming (49), and Osvald (30) restrict it to areas dominated by an ericaceous vegetation underlaid by a more or less continuous stratum of *Sphagnum* moss. Gates (19, p. 217)

[1] *Manuscript received December 12, 1951.*
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stresses physical characteristics: ". . . a bog is an area of vegetation, developing in undrained or poorly drained situations, which by the development of a mat invading open water, forms a cover over a body of water". He completes the picture by citing floristic criteria: ". . . a bog may be defined as an area vegetated by a flora in which peat-forming types of plants (including certain herbaceous, ericaceous shrubs and coniferous trees) are particularly abundant."

Many authors, Pearse (31) and Rigg (38) for instance, base their definitions almost exclusively on physicochemical factors, thus including swamps and marshes and virtually excluding some authentic bogs. Potzger (32, p. 567) considers that the difference between swamp and bog "is best made on the basis of the nature of the soil", although he accepts Rigg's (34) and Kurz's (23) definitions. He goes on to define bog not only in relation to substratum "of organic origin (peat) formed *in situ*" but also to water table which is "at or near the surface".

Tarr and Martin (46) consider the bog as a kind of swamp: "A swamp is a part of the surface of the land which is wet and saturated with moisture though not usually covered with standing water. Some swamps are called marshes, bogs, muskegs."

One of the best definitions is given by Welch (51, p. 347): "The writer chooses to use the term bog to include those situations in which: (1) the water manifests different reactions (acid to alkaline) in different areas; (2) a marginal, semi-floating mat often exists (or may have existed at some time), composed of an aggregation of characteristic plants; (3) deposits of peat are invariably present." Here several sets of criteria are resorted to: physicochemical variables, soil dynamics, evolution of vegetation.

The *Committee on Nomenclature of the Ecological Society of America* (List P-1, 1933, cited by Carpenter (11)) emphasizes substratum and calls bog "that stage in the physiographic succession of an area during which its surface is entirely of living sphagnum, immediately under which is a fibrous brown peat composed mainly or entirely of partially disintegrated sphagnum, the habitat exercising a distinctly selective influence on its flora".

As can be seen from the above, there is no general agreement as to what bogs are. Different authors have emphasized different criteria. Indeed, in some cases, the criterion itself is only vaguely defined, especially as concerns vegetation, sometimes referred to as "characteristic" (in composition, in structure, or in physiology?).

In Table I we have attempted to bring together as complete a set as possible of the factors and elements that have been used to distinguish bogs from swamps. Perhaps most to be emphasized are the facts: (1) that local drainage patterns are modified by bogs; (2) that the "soil" is of organic materials formed *in situ*; (3) that the general physiognomy is curvilinear.

It is, of course, recognized that all bogs and swamps respectively will not cumulate all the features mentioned. It is our conviction, however, that few truly intermediate cases are known. It may be well to emphasize that we are

TABLE I

THE CONTRASTING CHARACTERS OF BOG AND MARSH–SWAMP ECOSYSTEMS

Bog	Marsh and Swamp
PHYSIOGRAPHY	
Blocked drainage causes an indefinite accumulation of organic materials; a small quantity of mineral soil is introduced by seepage, inwash, and atmospheric agents.	Drainage pattern does not allow a considerable accumulation of organic materials; the shallow substratum and seepage permit a thorough mixture of organic and mineral sediments.
Drainage is further congested by the growth of a bog; several small bogs can thus unite and modify the drainage pattern over a fairly large expanse. This process is reversed only in the very late stage, when trees cover the area.	Drainage is gradually, if slowly, improved by the growth of swamp vegetation and the corresponding sedimentation.
Open water is invaded by a floating mat and pools are filled in from top as well as from bottom.	Open water is mostly invaded by nonfloating vegetation and filling-in is from bottom upwards.
PHYSICAL CONDITIONS	
Water table reaches the surface in the spring and is below the surface during the rest of the year. Often, phreatic level is just below the surface in the spring and considerably lower in midsummer.	Water table well above the surface in the spring and just at surface or little below it during the rest of the year.
Water surface often discontinuous when above soil level.	Water surface continuous when above soil level.
Adjacent open water generally brownish (dystrophic).	Adjacent open water generally turbid, olive-green or dark green (eutrophic).
Substratum cohesive, resilient, can uphold considerable weight (e.g. man).	Substratum soft, will absorb heavy objects, will not resist pressure.
Substratum almost 100% organic and always in the form of peat; mineral content low.	Substratum with variable percentage of organic materials, usually not peat; mineral content high.
A false bottom forms in open water, owing to accumulation of colloids.	No false bottom.
CHEMICAL CONDITIONS	
Predominance of strongly acid reaction. Percentage of saturation low. Large quantity of colloids in suspension.	Acid or alkaline reaction. Percentage of oxygen saturation high. Small quantity of colloids in suspension.
Potassium and nitrogen deficient in soil (although some nitrogen-fixing bacteria).	Potassium and nitrogen not deficient.
VEGETATION	
Presence (at some time) of a floating mat usually dominated by ericoid plants.	Mat, when present, composed of graminoid plants.
Physiognomic dominance of curvilinear contours: much-branched shrubs, cushionlike tufts of herbs and mosses, etc., curved surface of raised bogs.	Physiognomic dominance of rectilinear contours: graminoid herbs, flat surface of soil.

TABLE I—*Continued*

Bog	Marsh and Swamp
VEGETATION—*Continued*	
On the whole, a bog is a large cushion.	On the whole, a swamp is a wet prairie.
Dominance of the ericaceous type in many of the pioneer stages.	Dominance of the graminoid type in the pioneer stages.
Dominance of needle-leaved types in the subclimax stages.	Dominance of broad-leaved types in the subclimax stages.
Vegetal cover continuous, uneven, forming cushions, eventually parklike.	Vegetal cover discontinuous, in tufts or individuals isolated, eventually thicketlike.
Chamaephytes dominant in early stages.	Helophytes, geophytes, and hemicryptophytes dominant in early stages.
Mosses (mostly *Sphagnum*) always forming the lowest layer.	Mosses (at least *Sphagnum*) generally absent.
FAUNA	
Animal life scarce, both in numbers of species and of individuals.	Animal life abundant. Both in species and individuals.

here dealing with the palustrine habitat and not with bog lakes.* We would also point out that Table I lines up the elements of a static description and merely touches upon the dynamics without offering an answer to the question: What sets off the processes of bog vs. swamp formation in the first place?

Bog Formation

It is well, at this stage, to consider the phenomenon of bog formation before the phytosociological units are described.

Recently glaciated areas are favorable to the production of bogs: fluvioglacial deposits (drumlins, eskers, ponted moraines, etc.) act as barriers and produce irregular drainage patterns which result in a scattering of small lakes and basins (de Martonne (27), Lobeck (26)). The effects of erosion are more evident in alpine glaciation where arenas, warts, and suspended valleys are formed. Blocked drainage in all of these situations, combined with a cold climate and constantly high humidity, favor the accumulation of slowly decomposing organic materials known as peat.

The tropics have few bogs, as their high temperatures are usually combined with great evaporation and relative humidity is likely to vary too much. Many described tropical "bogs" are more likely swamps. But the mountains--and especially the fog belts—with lower temperatures and more

** Some limnologists will probably disagree, as they consider the lake and its consolidated mat as a single unit.*

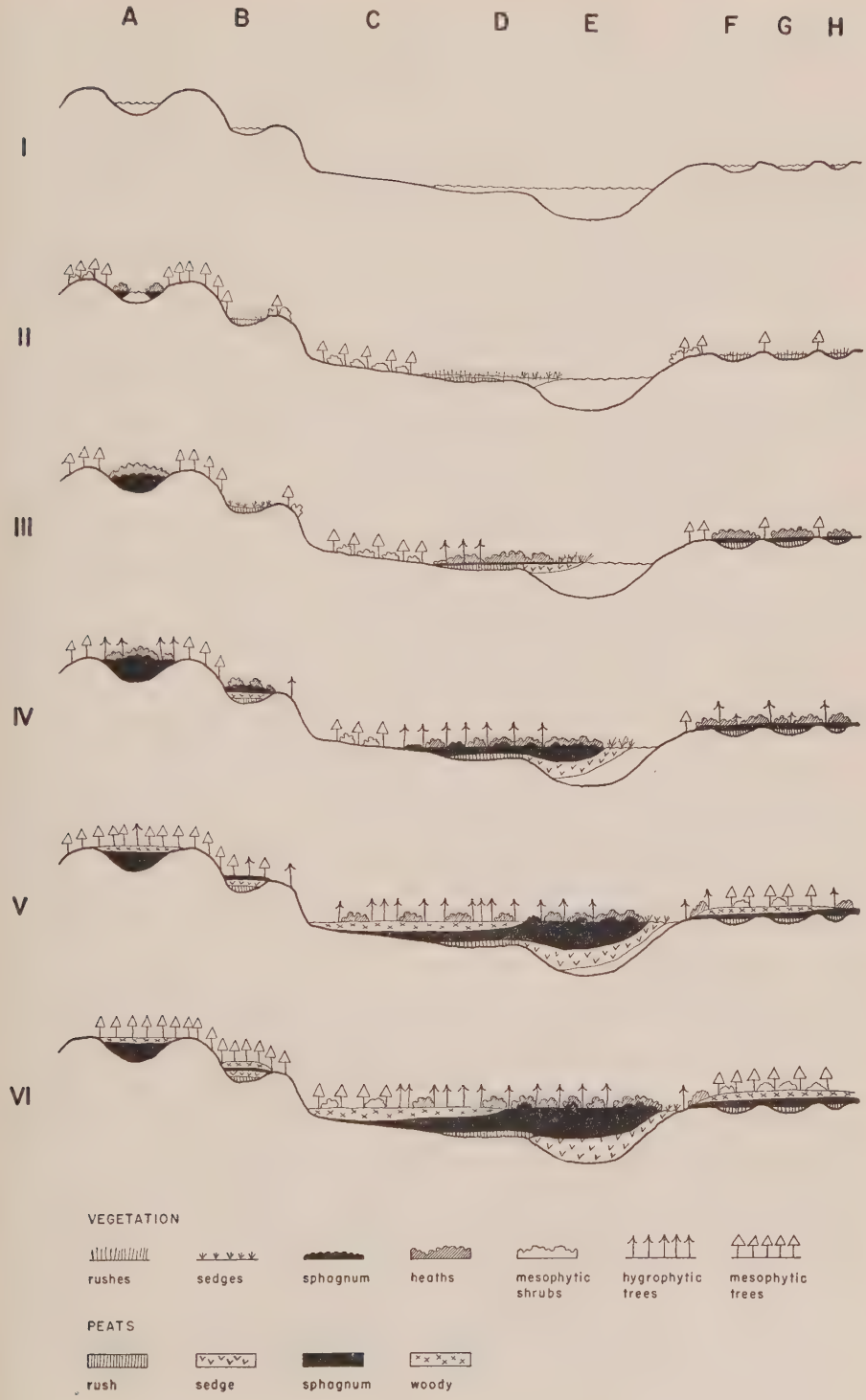
constant humidity, do have authentic peat bogs, for instance in the Belgian Congo, Abyssinia, Hawaii, and Southeastern Brazil.

An initial obstruction of drainage, therefore, is essential to the establishment of bog conditions. The substratum of the more or less closed basin (of varying dimensions: a mere pool or a large lake, a narrow trough or a long valley) can be rock, sand, or clay. It may be deep or shallow but it will always provide an inadequate outlet for the quantity of water which it gathers and will show practically no circulation. The reduction of wind action in these closed-in areas may also be important, as it will check the aeration of free water and favor anaerobic decomposition.

Probably the most significant feature of bogs (in contrast to swamps, see Table I) is that during the entire period of growth, drainage deteriorates consistently up to the point when a tree cover prevails and pumps up enough water to lower the phreatic level. Transeau *et al.* (47) state that bogs can actually invade forested areas and kill (mesophytic ?) trees. Potzger (32) describes a case where a beech stand was thus invaded. This idea had been advanced by several authors (v.g. Anderson and Hesselman (2)) and was used again recently by Rigg and Strausbaugh (44). The latter quote Auer (3) and apply his term of *paludification* to this process. In fact one wonders how far paludification can proceed actually. For instance, in a relatively extensive and almost flat area, natural drainage will fill small pools or at least maintain them saturated with water the year round. Early colonization is likely to be by rushes and sedges which will form a more or less stagnant marsh. *Sphagnum* will eventually creep into these areas and beyond their rims and extend a little higher on the flanks of the more or less dry mounds or ridges that separate them. They will then unite and form larger expanses of continuous *Sphagnum*. In the process, the more mesophytic or sometimes even xeric vegetation of the ridges will be destroyed and replaced. Such will be the case also of marginal areas. The whole bog can be compared to a sponge: the loose texture, the lightness of the materials of the "soil" and its enormous water-retaining capacity will allow it to grow to great proportions, a phenomenon which does not occur in swamps. These processes are outlined in Fig. 1 which illustrates a typical transect on the Laurentian Shield and adjacent sedimentary areas. The deposition of the different kinds of peat is seen to occur in various patterns of stratification.

There is, however, a limit to this mechanism of bog growth, a point where the rate of increase of the evaporating power of vegetation becomes greater than the rate of water-retaining capacity of the peaty mass. At that point, the natural regression which has taken place, at least over part of the area, is checked and progressive succession sets in and tends to drier, more mesic conditions. Of course the dynamics are again reversed if, through lumbering,

FIG. 1. A diagram of the probable evolution of bogs on the Laurentian Shield, reading from top to bottom (I to VI) and showing the processes that operate in the case of closed drainage (*A*, *B*, *F*, *G*, *H*) and in situations where there is more seepage or water movement and wind action (*C*, *D*, *E*).


A
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VEGETATION
rushes
sedges
sphagnum
heaths
mesophytic shrubs
hygrophytic trees
mesophytic trees
PEATS
rush
sedge
sphagnum
woody

fire, windfall, or other agencies, the tree layer is destroyed or much reduced. The rise of the ground water then induces paludification in the truest sense.

It must be added that geomorphological evolution, and especially the progress of erosion which may liberate certain local drainage systems by forging new outlets into the bog, will have the same retrogressive effect. This seems to have happened in the case studied by Potzger (32). On the other hand, renewed sedimentation or the influx of a new stream will serve to check or to reverse the trend.

The relative position of sedge, sphagnum, and woody peat layers in the bog profiles published by many authors show the alternance of progressive and regressive evolution in a very large number of cases and the frequent passage from marsh to bog (see especially Auer (3) and Rigg and Richardson (43)).

Bog succession has long been known in its broader aspects and Dachnowsky-Stokes' (15) diagram is now famous and has been reproduced in many texts (for instance Lobeck (26)). In the initial stage of bog formation, a floating mat is often formed which propagates vegetatively. The outward extension of the mat over open water is possible only if an already consolidated mass of peat exists or if a rock, a rotting log, or some solid object can serve as an anchoring point (Chouard and Prat (12)). Four transects across typical bog mats in our area are shown here as Fig. 2. The pioneer plants are often *Menyanthes trifoliata* and *Myrica gale*, although in some cases various *Cyperaceae* will serve that function. These plants form a loose tangle at first. Species of *Chara* often contribute to increase consistency. *Hypnum* and *Sphagnum* eventually grow in tufts about the stems of *Myrica*. Gradually, less hygrophytic species invade (such as *Chamaedaphne calyculata*) and open water-spaces disappear between the plants at the surface. It is some time, however, before the accumulation of peat below the surface consolidates. So that, at a relatively advanced stage of succession (v.g. *Piceetum ericaceum*), the bog may still be on a floating mat. The weight of accumulating peat causes a gradual sinking and eventual filling to the bottom. Decomposition is checked by immersion, and the fibrous sphagnum peat often contains almost intact pieces of wood.

We have attempted, in Fig. 1, to apply these principles to the evolution of bog vegetation on the Laurentian Shield. Positions *A*, *B* and *F*, *G*, and *H* show small, self-contained basins where vegetation rapidly establishes control of drainage. In *F*, *G*, and *H* much mesophytic vegetation is destroyed in stages III and IV. In *C*, the slow seepage from above allows mesophytic plants to colonize; they are later to be displaced (in stages IV and V) by bog growth, until the process is reversed (in stage VI).

Another process consists in the sedimentation in the open water of extremely fine particles, or of even larger portions either from dead aquatic vegetation, already formed peat, or atmospheric dust, pollens, minerals, etc., or even cosmic dust. In this case, sedimentation is constant and slow and produces a fine-textured peat, sometimes with a fairly high mineral content. The slowness of this process does not allow it the same dynamic value as that of

the one described above (Lobeck (26)). Also the particles, in the course of their transition from the water surface to the bottom, can be oxidized, decomposed, or can remain in suspension as colloids. These small bodies are subject to considerable movement and will often remain in solution until they are precipitated either by chemical, bacterial, or photosynthetic causes. This type of sedimentation is related not only with certain types of aquatic vegetation but also with a local physiography which allows allochthonous materials to reach water surface. They are eventually deposited in the so-called false bottom (see Fig. 2).

The evolution of vegetation is, of course, parallel to the filling-in of the water area and its structure is parallel to the physiographic stages of evolution. Chouard and Prat (12, 13) have shown that, in the Pyrenees, the advance of the mat is not a totally irreversible phenomenon, at least where the neighboring slopes are calcareous. The consolidated peat, when infiltrated by alkaline water, will, in fact, ferment and disintegrate, so that pockets will form beneath the surface and cause sagging and caving in. Lewis and Dowding's (24) Fig. 4 shows the same phenomenon in Alberta and the resulting hummocky structure of a zone of vegetation. A similar regression may take place where there is still an area of open water, or where a recent fire has broken down the windbreaks, and, of course, where the local physiography itself is rapidly changing (Potzger (32)). In all cases, a new mat may form and be subject again to the same influences. The constant recurrence of this mechanism may inhibit the sealing up of a bog lake, in such a way that the evolution of the mat in Position *E* of Fig. 1 will stop at stage III or that a cycle from III to IV and back to III will prevail.

Chouard and Prat (12) have analyzed the dynamics of mat formation in Pyrenean lakes. They have observed the buoyancy of such plants as *Menyanthes*, and their role in the extension of the mat. They have greatly emphasized the buffer effect of various *Hypnaceae*.* These mosses occupy the outer fringe of the mat, an area which shows a pH of 6.0, whereas the open water reaches 7.4 to 8.0 and the inner part of the mat (where *Sphagnum* is present) is down to 4.0-5.0! They conclude that *Sphagnum* cannot invade alkaline water directly but can only follow upon previous acidification by a more alka-tolerant organism. Potzger (32) also concludes that *Sphagnum* does not acidify the soil with which it comes in contact.

Other authors (Rigg (38, 39)) believe that *Sphagnum* itself can acidify the environment: "sphagnum causes water with which it remains in contact to have an acid reaction. This is true not only of living sphagnum but also of its dead remains". Baas-Becking and Nicolai (4) agree with Bauman and Gully's (5) theory, who "consider the cell wall to be a colloid which when placed in a salt solution, adsorbs the kations exclusively and sets free the acid." Thus hydrogen-ions are left free through an exchange of ions between *Sphagnum* cells and the solution.

* *Hypnum stramineum and H. fluitans; also, H. stellatum, H. vernicosum, Fissidens osmundoides, and the liverwort Scapania undulata.*

The open water adjacent to the bog mat may therefore present various reactions, from alkaline to acid. Gorham (20) considers these to be due to organic materials in suspension and to free carbon dioxide or to mineral acids. In the midst of *Sphagnum*, water is always acid. However, acidity of the peat "soil" seems to decrease with depth (Potzger (32, 33)). This obviously still leaves great uncertainty as to the features *initially* favorable to invasion by *Sphagnum*.

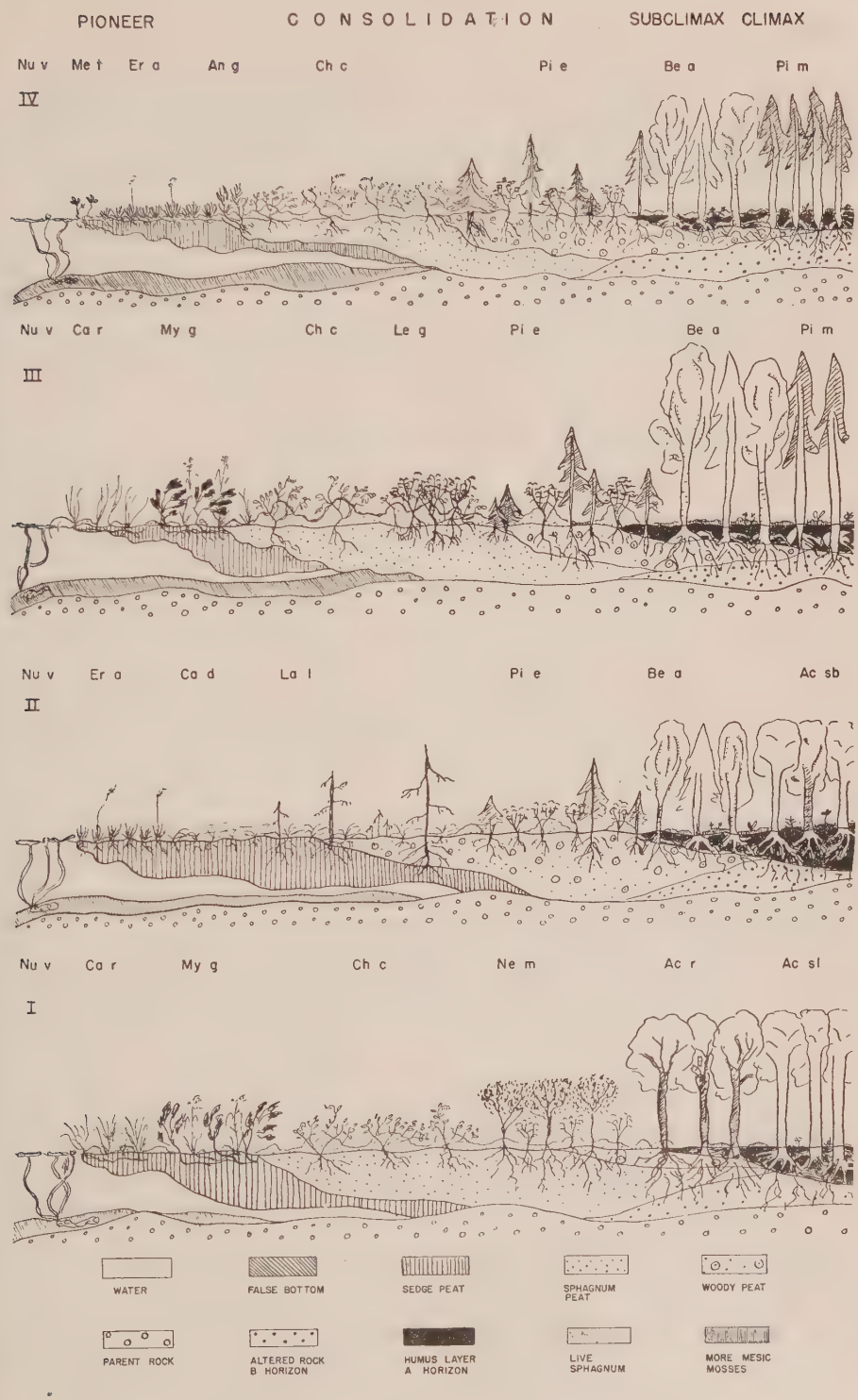
Such are, briefly outlined, the forces at work in bog formation. They have been studied in many areas, and *progressive* and *regressive* successions have been described. Many suggestions have been made as to the *checks* that occur in the course of succession and that prolong the existence of a certain stage, as it seems, indefinitely. Also the factors which apparently tip the scales in a progressive succession and initiate a regressive or deflected one can be variously interpreted. We hope, in the course of the present series of studies, to be able to contribute to an understanding of the dynamics of bog formation and evolution in Eastern North America, to compare the situation here with that of Western North America (Rigg and Richardson (43)) and of Northern Europe, and to apply Osvald (29) and Kulczynski's (22) classifications. We have very many *kinds* of bogs in our area and they vary with latitude, continentality, and altitude, as well as with changing drainage patterns. Their relation to both topography and surrounding vegetation thus undergoes several shifts.

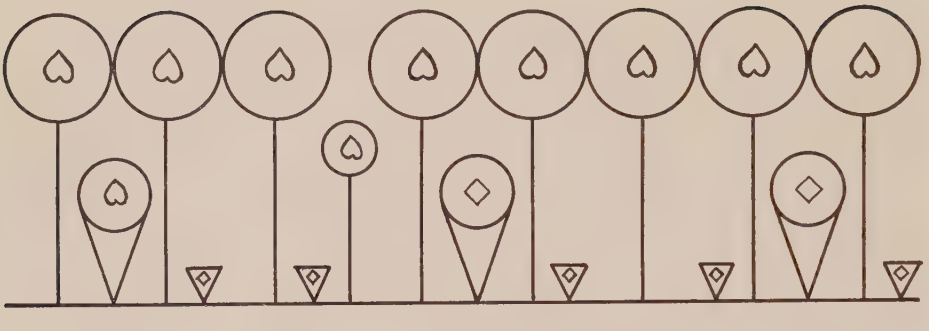
However, our first task consists in conveying a picture and producing an analysis of our bog communities. It will therefore be our purpose to describe these associations, first as to structure, physiognomy, synecological relationships, and dynamic status and then as to phytosociological composition and characteristics. In doing so, we shall have to work under a certain number of assumptions that will, in the end, be questioned. This includes the definitions and principles expressed above which we hope to be able to recast later in sharper outline at least in relation to the area considered.

Bog Associations: Their Structure and Dynamics

Reference to a plant association must always imply three main considerations: structure, composition, dynamics. In all three respects, there are conspicuous differences between the communities of the *early stages*, the *consolidation period*, and *forest invasion*. Different modes of *disturbance* must also be considered. Fig. 2 shows four bog transects in the Province of Quebec: I and II are taken in the St. Lawrence Lowlands and illustrate both zonation and succession to a hardwood climax (see diagram in Figs. 3 and 5); III and IV show the situation in the Canadian Forest zone (see diagram in Figs. 4 and 6).

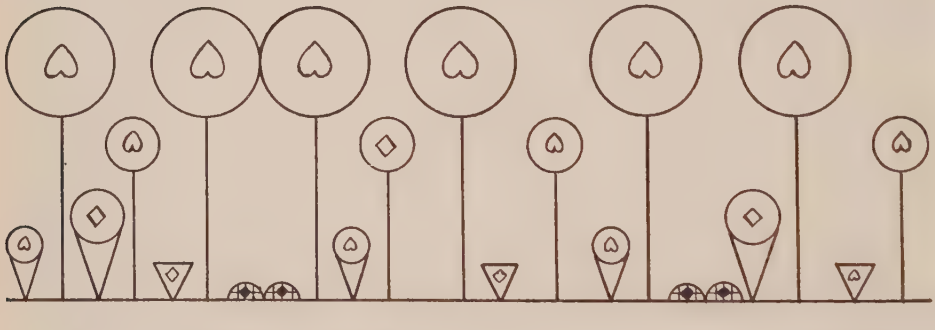
FIG. 2. Four typical transects through bogs of the St. Lawrence Valley, illustrating the relative positions of the principal communities of the zonation, which are generally also related in succession. The symbols immediately above each vegetation type are abbreviations of the names given in Figs. 5 and 6. Transects I and II, ending in a deciduous forest climax represent the St. Lawrence Lowland area, whereas Transects III and IV show the Canadian Spruce–Fir forest area.


PIONEER
CONSOLIDATION
SUBCLIMAX CLIMAX
Nu v Me t Er a An g Ch c Pi e Be a Pi m
IV
Nu v Ca r My g Ch c Le g Pi e Be a Pi m
III
Nu v Er a Ca d La l Pi e Be a Ac sb
II
Nu v Ca r My g Ch c Ne m Ac r Ac sl
I
WATER
FALSE BOTTOM
SEDGE PEAT
SPHAGNUM PEAT
WOODY PEAT
PARENT ROCK
ALTERED ROCK B HORIZON
HUMUS LAYER A HORIZON
LIVE SPHAGNUM
MORE MESIC MOSSES



ACERETUM SACCHAROPHORI

Ttdhzc. Tldhzb. Ftda(h)zi. Hldazi.



ACERETUM RUBRI

Ttdhzc. Tldh(a)zi. Fmdazb. Fldhzi. Hlda(h)zi. Mlenxp.

NEMOPANTHETUM MUCRONATAE

Fmdazp(hzb). Flsaxp. Mmeafp. Mleafp.

CHAMAEDAPHNETUM
CALYCULATAE

Fmenxb. Flsaxc. Mmeafc. Mleafp.

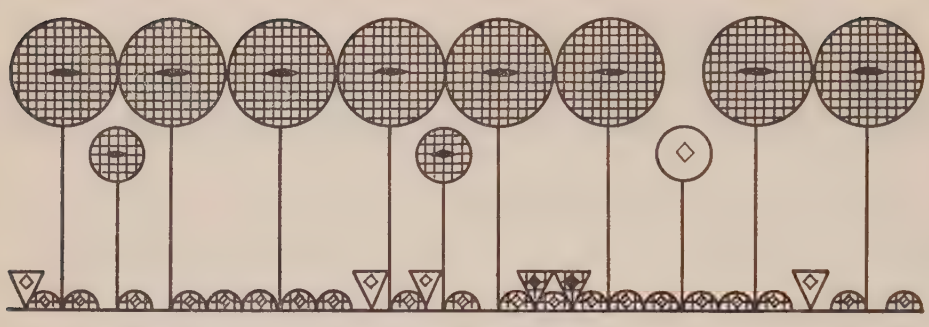
MYRICETUM GALEAE

Fldazp. Hmdgxi. Hldgzb. Mleafb.

CARICETUM ROSTRATAE

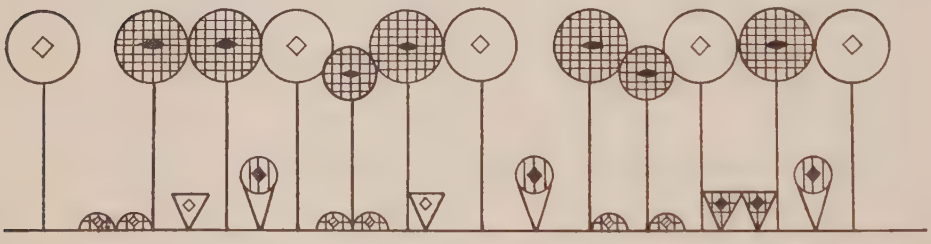
Fldazb. Hmdgxc.

FIG. 3. Transect I of Fig. 2 plotted according to the system outlined in Table III (Dansereau (18)).



PICEETUM MARIANAE

Ttenxc. Tlenx(daz)i. Hldazb(eaxp). Mleafc.



BETULETUM ABIETOSUM

Tmdaz(enx)c. Tlenxi. Flsaxi. Hleax(daz)i. Mleafp.

PICEETUM ERICACEUM

Tl(Ft,Fm)enxi. Flsaxp. Mm(l)eafc.

LEDETUM GROENLANDICI

Fmenxb. Flsaxc. Mmeafp. Mleafp.

CHAMAEDAPHNETUM CALYCULATAE

Fmenxb. Flsaxc. Mmeafc. Mleafp.

MYRICETUM GALEAE

Fldazp. Hmdgxi. Hldgzb. Mleafb.

CARICETUM ROSTRATAE

Fldazb. Hmdgxc.

FIG. 4. Transect III of Fig. 2 plotted according to the system outlined in Table III (Dansereau (18)).

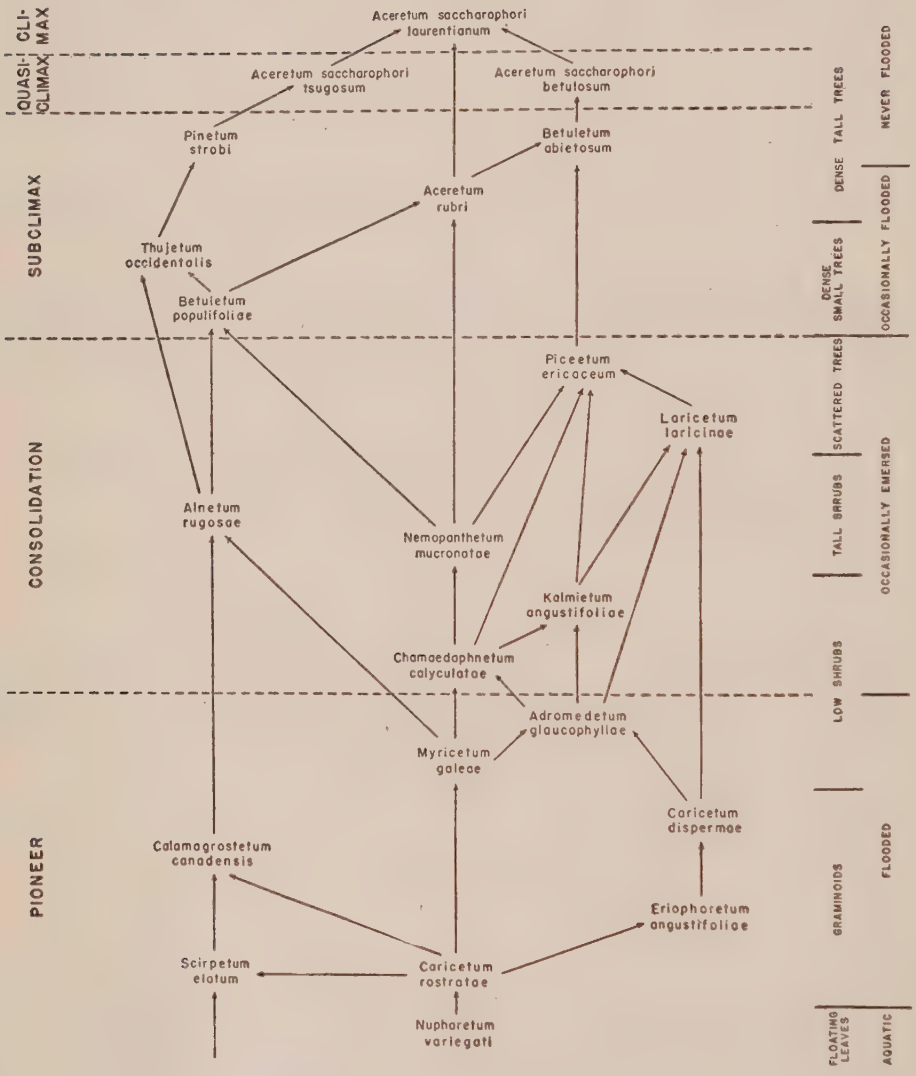


FIG. 5. Diagram of succession in the St. Lawrence Lowlands, where the climax is deciduous forest. The controlling ecological factors corresponding to the major phases are indicated, as is also the dominant structural unit.

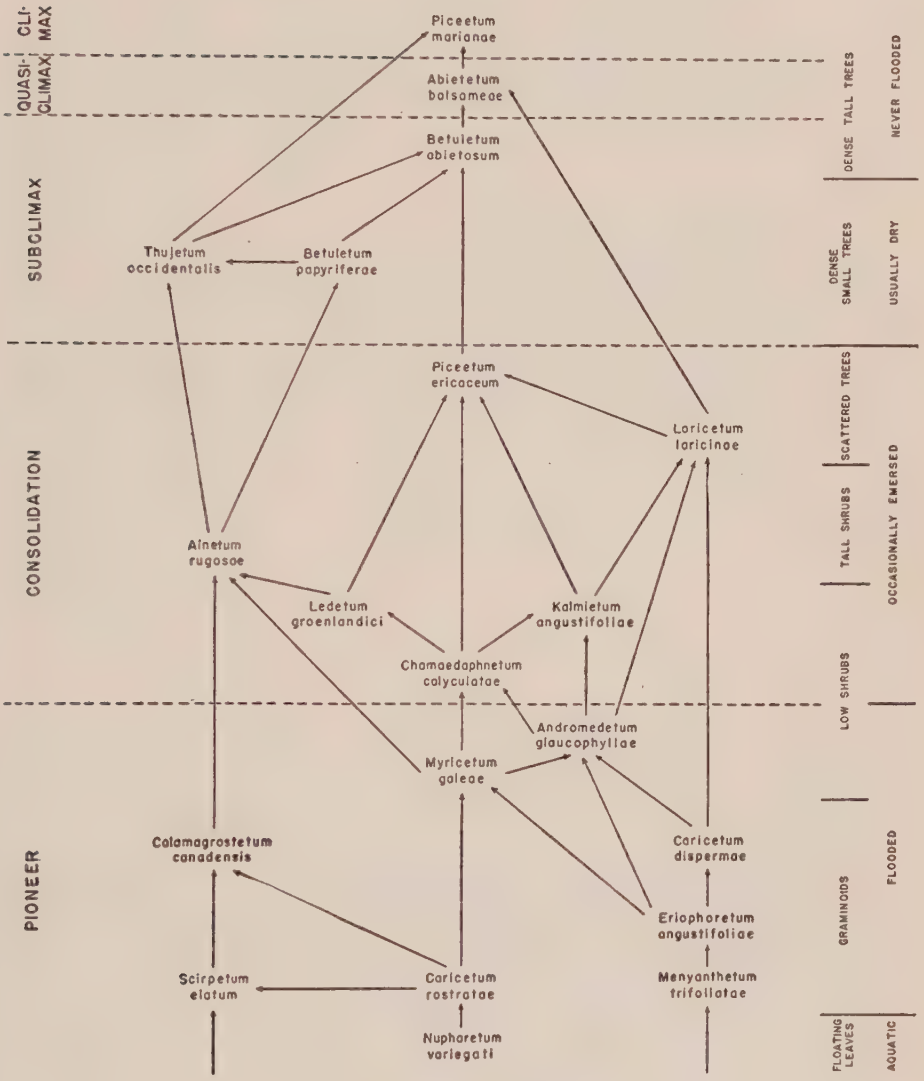


FIG. 6. Diagram of succession in Northern Quebec and Ontario where the Canadian or Spruce–Fir forest is climax. Principal features of structure and controlling ecological factors are shown for each major phase.

FIG. 7

FIG. 8

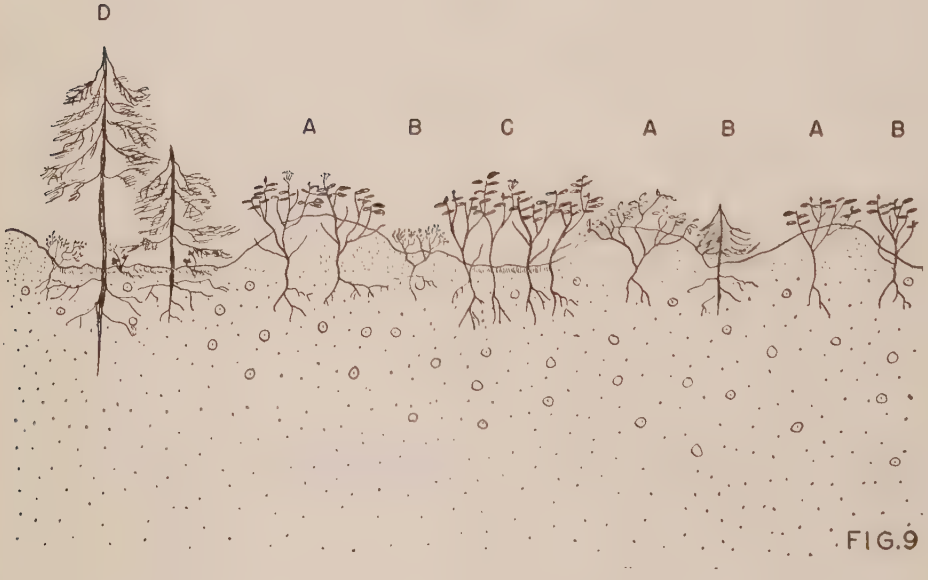


FIG. 9

TABLE II

KÜCHLER'S PHYSIOGNOMIC CLASSIFICATION OF VEGETATION (21)

Capital letters

Woody vegetation	Herbaceous vegetation
B: evergreen broadleaf	G: graminoids
D: deciduous broadleaf	H: forbs
E: evergreen needleleaf (coniferous)	L: lichens and mosses
N: deciduous needleleaf (coniferous)	
O: without leaves	

Small letters

Group I: Height	Group II: Density	Group III: Special features
t: tall; minimum height of trees: 25 m. minimum height of herbaceous plants: 2 m.	c: continuous growth	e: epiphytes
m: medium tall; trees: 10-25 m. herbaceous plants: ½-2 m.	i: plants usually do not touch	j: lianas
l: low; maximum height of trees: 10 m. maximum height of herbaceous plants: ½ m.	p: woody plants scattered singly or in groves herbaceous plants in disconnected patches	k: succulents
s: shrubs; minimum height: 1 m.	r: rare, yet conspicuous	q: cushion plants
z: dwarf shrubs; maximum height: 1 m.	b: barren; vegetation largely or entirely absent	u: palms
		v: bamboos
		w: aquatic vegetation
		y: tree ferns and tuft plants

Let it first be stated what we understand by structure: *the arrangement in space of the different synusiae.* A red fescue meadow and a poverty-grass sward may have the same structure, as will a white birch and an aspen stand, whereas they differ in composition. Plant associations of the same structure are often at comparable levels of succession. One of us (Dansereau (18)) has elaborated elsewhere on the significance of a physiognomic and structural definition of vegetation types or plant communities, and has proposed a system

FIG. 7. A detailed view of the *Myricetum galeae* (see Fig. 2, I and III). The lower layer in the "soil" (widely spaced vertical lines) is well-decomposed peat; the upper layer (crowded vertical lines) is fibrous peat; whereas the small hummocks (oblique lines) are of living *Sphagnum*. These hummocks harbor many small herbs, such as *Lycopus uniflorus*. The open water biotope has few higher plants, sometimes a good growth of algae.

FIG. 8. A section through the *Chamaedaphnetum* (see Fig. 2, I, III, and IV).

FIG. 9. The various biotopes in a *Piceetum ericaceum* (Fig. 2, II, III, and IV). *A* is the high moss cushion prevalent in the *Chamaedaphnetum*. In *B*, the cushion has been somewhat flattened out and *Ledum*, *Vaccinium*, or *Picea* develop more freely. A dense growth of one of the shrubs, for instance *Ledum*, in *C*, even permits more mesophytic mosses (such as *Calliergonella schreberi*) to replace *Sphagnum*. In *D* is shown one of the islands formed by one or more individuals of *Picea mariana:* in their shade grow sylvatic mosses and herbs (for instance *Coptis groenlandica*).

of structural units, the key to which is given here as Table III. This had followed upon the publication of Küchler's (21) geographic and physiognomic system of vegetation (see Table II) to which it owes a good deal.

As will readily be seen on Table II and in Figs 3 and 4, six sets of criteria are used to describe plant communities without reference to actual botanical composition. This approach is best suited to allow a comparison of the structures of different associations, emphasizing stratification, coverage, leaf-shapes, and textures and degree of evergreenness. Figs. 3 and 4 thus show many contrasts.

Nomenclature will be according to composition: the dominant species providing a latinized association name according to the procedure of the Zürich and Montpellier School (Braun-Blanquet and Pavillard (9)).* Two groups of symbols follow that designate and represent the essentials of the structure of the community, the first (upper line) according to Küchler's system (21) as shown on Table II and the second (lower line) according to Dansereau's (18) as shown on Table III. It has been found useful to separate the synusiae in both cases by a period, thereby more definitely emphasizing stratification. Some of the associations have been further illustrated by diagrams corresponding to the formulae of Dansereau (18). A group of these are shown on Figs. 3 and 4. In a few cases, more detail is shown so as to emphasize the importance of biotopes (Figs. 7, 8, 9).

In each case, the physical conditions of the community will be outlined, also its place in the sere and its relation to neighboring associations (see Figs. 5 and 6). The principal plant species will be named and in some cases their behavior and restriction to a biotope will be described. Occasional references will also be made, for purposes of comparison, to descriptions given by other writers.

Three major phases will be considered: the *pioneer*, *consolidation*, and *forest* periods. Figs. 2, 3, 4, 5, and 6 show the principal steps in succession of bog vegetation, from open water to the forest climax in the Laurentian forest (or St. Lawrence-Great Lakes, or Northern Hardwood area) (Fig. 5), and in the Canadian (or Boreal, or Spruce–Fir area) (Fig. 6).† Modifications in structure will be emphasized especially, as will also their correlation to microclimatic changes. Only the abundant or indicator species need be mentioned for the moment, as complete phytosociological analysis of most of the associations will follow in later papers.§

* *In a recent review of a paper by the senior author, H. M. Raup (Quarterly Review of Biology, 24 (2) : 141-142. 1949) disapproves of this nomenclature as unduly stressing the assumed analogy between the community and the plant species. I would like to say that although the organismal nature of the community is implied in most of the writings of the "Zürich and Montpellier school", it need not necessarily be linked to the purely descriptive use of latinized nomenclature. Personally I do not make such a connection and unhesitatingly reject the idea of the community as a superorganism. P.D.*

† *In a forthcoming paper in this series the relation of bog communities to regional conditions and vegetation will be studied in greater detail. It seems to me that the St. Lawrence Lowlands are part of E. L. Braun's (8) Beech–Maple and not White Pine-Hemlock Northern Hardwoods area. P.D.*

§ *The Chamaedaphne calyculata community in Quebec and Ontario by Fernando Segadas-Vianna is Number II of this series.*

TABLE III

THE SIX CATEGORIES OF CRITERIA TO BE APPLIED TO A STRUCTURAL DEFINITION OF VEGETATION TYPES (DANSEREAU (18)).

1. LIFE-FORM

T trees
F shrubs
H herbs
M bryoids
E epiphytes
L lianas

2. SIZE

t tall (T: min. 25 m.)
(F: 2-8 m.)
(H: min. 2 m.)
m medium (T: 10-25 m.)
(F,H: 0.5-2 m.)
(M: min. 10 cm.)
l low (T: 8-10 m.)
(F,H: max. 50 cm.)
(M: max. 10 cm.)

3. FUNCTION

d deciduous
s semideciduous
e evergreen
j evergreen-succulent or evergreen-leafless

4. LEAF SHAPE and SIZE

n needle or spine
g graminoid
a medium or small
h broad
v compound
q thalloid

5. LEAF TEXTURE

f filmy
z membranous
x sclerophyll
k succulent or fungoid

6. COVERAGE

b barren or very sparse
i discontinuous
p in tufts or groups
c continuous

In the course of plant succession on any terrain there are usually several shifts in the control of communities by habitat factors. In other words the prevalent influence may be successively of water availability, soil reaction, shade, and germinating capacity of dominant plant species. This shift of the major influence has allowed Huguet del Villar (48) to propose a classification based on discrepant factors (see English translation in Dansereau (18)). By analogy with geological phenomena one may consider the points of relay from the determinating influence of one factor to that of another as an *unconformity*. Several of these appear in the course of a bog succession, the most important ones being at the initial point of each of the three major phases (see Figs. 2, 5, 6).

THE EARLY STAGES OR PIONEER PHASE

Most bog successions have an initial aquatic phase. This is not really part of the bog sere, or not exclusively so, as these communities are just as

conspicuous in riparian seres. They are all situated in conditions of very nearly permanent flooding, the first three being actually under water long enough to harbor many true aquatics.

Nupharetum variegati (Fig. 2)

H l i w

H l d h z i

The floating-leaved life-form (N of Dansereau (16)) dominates here, with *Nuphar variegatus* (or *microphyllus*, *rubrodiscus*), *Nymphaea odorata*, *Potamogeton natans*, *Sparganium americanum*. These plants root in the false bottom, or in the unconsolidated ooze resulting from plant deposits either of the *Nupharetum* itself or of neighboring belts of vegetation, or of previous occupants. This association, and its equivalents throughout the boreal hemisphere, owe their position in the transect more to organic sedimentation than to actual depth of water (see comparison of many stations in Europe and North America in Dansereau (16, Table III)).

The accumulation of plant detritus accelerates the filling-in process, consolidates the false bottom and raises the floor of the lake. Organic decomposition will tend to reduce the quantity of available oxygen and to produce toxic substances. Thus there will be a greater accumulation of peat. Some of these organic substances will remain in suspension in the form of colloids, giving origin to the acid and alkaline reactions which have been observed in bog lakes (Gorham (20), Welch (52)).

Filling-in will favor the establishment of *Caricetum rostratae*.

Menyanthetum trifoliatae (Fig. 2, IV)

H l p w

H l d v z p

Menyanthes trifoliata var. *minor* (North American vicariant of the European *M. trifoliata* var. *trifoliata*) is a very exclusive species, narrowly specialized to its position on the outer edge of the floating mat, where it forms a consociation. Its soft floating rhizomes build a rather loose and flexible network, very resilient under water-level fluctuations, and wind-induced water movements. This outer belt of vegetation (usually not very wide) thus contributes to check aeration and therefore to slow down decomposition of organic matter.

Upon the rhizomes, little by little, algae and *Chara* will become enmeshed and will tend to reduce the free spaces, thereby producing conditions favorable to species intolerant of an unconsolidated substratum, such as *Comarum palustre*, *Calla palustris*, and even *Geum rivale*. These are often present at the inner edge of the *Menyanthetum*, sometimes associated with bog species of higher requirements such as *Vaccinium oxycoccos*, *Eriophorum virginicum*, *E. angustifolium*, *E. spissum*, and even *Chamaedaphne calyculata*.

Hypnum is often present towards the outer edge and *Sphagnum* towards the inner. Chouard and Prat (12) have emphasized the pH buffer effect of *Hypnum* (see above).

This association does not occur in all bogs nor in bogs only. In Europe it appears to have the very same structure although a few minor floristic elements are different (Osvald (28)).

Caricetum rostratae (Fig. 2, I and III; Fig. 10)
G m c w
H m d g x c

This association is dominated by tall sedges: *Carex rostrata*, *C. lanuginosa*, *C. lasiocarpa*. These plants are rhizomatous and not tussock-forming. They are commonly of a pale yellow-green. The community is generally unistratal (see Figs. 2, I and III; 3; and 4). It occupies a narrow band (Fig. 10), in shallow water, usually in places where peat comes in contact with sand or some other predominantly mineral substratum and where there is quite a fluctuation in water level, to the point of emergence in the late summer. *Iris versicolor* is frequently present at the inner edge and will sometimes develop into a separate belt (Gates (19)) as it so often does on rocky or gravelly shores, especially towards its northern limits.

Eriophoretum angustifolii (Fig. 2, II and IV)
G l c. L i
H l d g z c. M l e n f i

This wet meadow, dominated by *Eriophorum virginicum*, *E. angustifolium*, or *E. spissum* (according to latitude) has essentially continuous vegetation and favors the growth of *Sphagnum*. It is frequently on a floating mat, but sometimes occurs in consolidated areas where a high water level prevails throughout most of the summer. This latter condition seems due to human interference in most cases. Frequent associates are *Kalmia polifolia*, *Andromeda glaucophylla*, *Carex disperma*, *Vaccinium oxycoccos*, *Sarracenia purpurea*.

Caricetum dispermae (Figs. 2, II; 13)
G l c
H l d g z c

In structure, this association, dominated by the delicate *Carex disperma*, differs very little from the preceding, although it indicates drier or less fluctuating conditions. *Vaccinium oxycoccos* is present, and usually young individuals of *Larix laricina*. It thrives under somewhat reduced light: the sparse shade of larch upon the tufts of *Carex* seems to favor their propagation, whereas the fall or death of larch will permit an invasion by *Eriophorum* or *Chamaedaphne* (Fig. 13).

Myricetum galeae (Figs. 2, I and III; 7; 10)
D z c. G l r. L i
F m d a z c. H l d g z b. M l e n f i

The characteristic decumbent form of *Myrica gale*, well illustrated by des Abbayes and Hamant (1), reveals its mode of vegetative propagation and its role in the formation and consolidation of the mat. The coverage of this

species—alone of its life-form—attains 80%. Its height is generally less than 1 meter. It is favored, in an environment poor in nitrogen, by bacterial root nodules (Gates (19), Bond (6)). A few individuals of *Chamaedaphne calyculata* are restricted to the higher and drier biotopes. Some sedges, *Eriophora* and grasses (especially *Leersia oryzoides*, see Fig. 7) occur here and there, and tufts of *Sphagnum* cover tangles of *Myrica* stems. Soil is almost nonexistent, except where local deposits of *Sphagnum* form shallow peat. The water emerges in pools scattered throughout the association; it is generally acid. In fact, the buffer effect mentioned in the case of the *Menyanthetum* is also active here, at least in alkaline lake areas, such as that described for Brittany by des Abbayes and Hamant (1). This association, although it generally invades one of the three preceding, will very often directly reach out into open water.

It is very commonly succeeded by the alder bush (*Alnetum rugosae*), and this is prefaced by the development of biotopes of a sylvatic character (Fig. 7), in the immediate shade of the *Myrica* foliage. Here such plants as *Lycopus uniflorus* and even *Onoclea sensibilis* will develop.

Andromedetum glaucophyllae (Fig. 2, IV)

D z c. L i

F l d a x c. M l e n f i

The species *Andromeda glaucophylla* is present in most ericaceous bogs, but the conditions immediately favorable to its establishing dominance are somewhat unusual. The optimum range of its water requirements and tolerances seems to overlap those of *Myrica gale* towards the maximum and those of *Chamaedaphne calyculata* towards the minimum. It frequently occurs, therefore, as indivuduals or in very small patches in the driest parts

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FIG. 10. Canadian Forest bog lake in the Upper Peribonka (Quebec). The *Caricetum rostratae* extends into open water, whilst the *Myricetum galeae* forms the next belt. *Alnetum rugosae* immediately precedes the forest (*Piceetum marianae*). This is a somewhat telescoped zonation, lacking good development of the *Chamaedaphnetum* and of a birch belt.

FIG. 11. A view from above of the *Chamaedaphnetum* shown in Fig. 8. The twigs of the heath, both living and dead, emerge from the moss cushion: left of center, *Chamaedaphne calyculata*; center and top center, *Ledum groenlandicum*; lower right, *Vaccinium angustifolium*.

FIG. 12. In the foreground, a dense *Chamaedaphnetum* maintained by fire. In the background a mature *Laricetum*. Alfred, Ont.

FIG. 13. *Sarracenia purpurea* and *Ledum groenlandicum* on a mat of *Carex disperma*, in the *Laricetum* shown in Fig. 12.

FIG. 14. A well-developed *Chamaedaphnetum* in the process of invasion by *Piceetum ericaceum* at Actonvale, Que. *Picea* and *Larix* both abundant in the invading community. At extreme right, a belt of *Betuletum abietosum*. (Photo by Harry Lash.)

FIG. 15. A late stage in the *Piceetum ericaceum*, where the spruce is closing in upon *Ledum groenlandicum* and *Kalmia angustifolia*. St. Blaise, Que.

FIG. 16. A typical Laurentides landscape, at Ivry, Que., showing the inner spruce belt and the outer deciduous belt around a still open leatherleaf bog.


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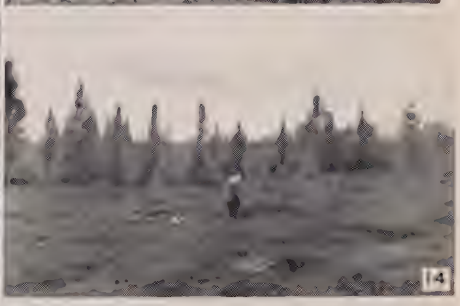
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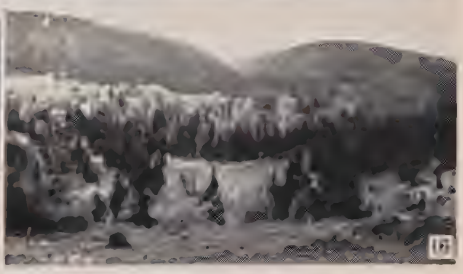
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of the *Myricetum* or the wettest of the *Chamaedaphnetum*. Only very occasionally do the physical factors (especially fluctuation of water level) permit *Andromeda* to form a separate belt between *Caricetum rostratae* or *Menyanthetum trifoliatae* or *Eriophoretum angustifoliae* and *Chamaedaphnetum calyculatae* or between *Myricetum galeae* and *Chamaedaphnetum calyculatae*. Probably the *Andromedetum* should be considered a mere facies of the *Chamaedaphnetum*.

The Consolidation Stages or Settlement Phase

A second phase is entered into with the definite establishment of a continuous *Sphagnum* "sod". The substratum itself will vary in composition and structure but not substantially in texture. The differences in botanical composition and in structure of the associations present will be due to fluctuations in water level, to raising of the surface through accumulation of moss and other vegetation (not much accumulation of dead tree trunks until the next, subclimax, phase).

Chamaedaphnetum calyculatae (Figs. 2, 3, 4, 8, 11, 12)

D z c. L c *
F l s a x c. M m e n f c

This association is one of the most widespread, the most extensive, and the most characteristic (Conard (14), Gates (19)). The apparently wide spectrum of *Chamaedaphne calyculata*'s tolerances also make it quite long-lived. As a matter of fact that species is probably more than any other a *bog species*, in that it combines the distinctions of being found in practically all boreal bogs; of being exclusively confined to the bog habitat; of usually being represented by large numbers of individuals; of withstanding for some time such diverse interferences as drainage and fire (Gates (19)). The upper synusia (40-60 cm. high as a rule) sometimes consists exclusively of *Chamaedaphne* which hardly ever grows more than 1.3 meter, and is usually very much smaller (30-50 cm.). It is a semideciduous shrub, the tips of its branches often nipped by winter frosts. It grows in groups of several individuals, has superficial roots, fibrous and without nodules (Gates (19)). Usually in the upper synusia there is a certain amount of *Ledum groenlandicum*, *Kalmia polifolia*, *Kalmia angustifolia*. A thin second synusia is sometimes formed by *Vaccinium angustifolium* especially following a burn. *Sphagnum* usually makes tremendous growth in the *Chamaedaphnetum*. In fact, it grows about the stem and branches of *Chamaedaphne* itself and forms a broad inflated cushion in which the subshrub is all but immersed (see Figs. 2, 3, 8, and 11). On the sides of these emergences and in the depressions between them (difference in level: up to 50 cm.), grow such plants as: *Vaccinium oxycoccos*, *Drosera rotundifolia*, *Sarracenia purpurea*. The *Chamaedaphnetum* occurs

** Küchler's formula D z is used here for Chamaedaphne as his system does not provide for semideciduous species but only for mixtures in a stand or area of evergreen and deciduous species.*

under a number of different facies; in some cases, it bears a strong admixture of *Ledum groenlandicum* or *Kalmia angustifolia* or *Eriophorum angustifolium*.

The substratum always shows a strongly acid reaction and, owing to the stools of leatherleaf and the moss cushions, has an uneven relief. Water content is still very high and water-retaining capacity of the living *Sphagnum* is likewise considerable. The underlying peat, however, presents a firm texture favorable to shrubs (such as *Aronia melanocarpa*, *Nemopanthus mucronata*) and even trees (*Picea mariana*, *Larix laricina*). These will eventually bring about more shade than *Chamaedaphne* can withstand and produce a *Piceetum ericaceum*, where only scattered individuals or small colonies of the leatherleaf will survive.

Very frequently, however, lumbering or fire will induce a regression and the *Chamaedaphnetum* will form anew (see also Gates (19)).

Ledetum groenlandici (Figs. 2, III; 4)

D z c. L p*
F l s a x c. M m e n f p

In somewhat less moist places, or possibly where water-table fluctuations are not so extreme, *Ledum groenlandicum* dominates. A perfect consociation is not usually found in the St. Lawrence Lowlands, where the establishment of large numbers of individuals seems precarious and unstable, in spite of the species' wide range of adaptation to both humidity and light. But it is fairly frequent in the Lake St. John area and on the Laurentian Shield.

Fig. 4 illustrates the difference in structure between the *Chamaedaphnetum* and the *Ledetum:* the *Sphagnum* cushions in the latter are depressed. Eventually, under dense clumps of *Ledum*, the more mesophytic mosses, for instance *Calliergonella schreberi*, become established. The progressive enlargement of this biotope is one of the principal features of progression to the *Piceetum ericaceum* (see Fig. 9, C).

Kalmietum angustifoliae

D z c. L p*
F l s a x c. F l d a z i. M l e n f p

In the Lower St. Lawrence Lowlands this consociation seems to attain its optimum. Bogs between Rivière-du-Loup and Rimouski sometimes show immense expanses of pure *Kalmia angustifolia* with only a very small quantity of *Ledum groenlandicum*. Here the superficial part of the soil may dry up completely in August, whereas it is saturated and even flooded in the spring. A second synusia of *Vaccinium angustifolium* is quite common and also harbors abundant *Rubus chamaemorus*, the always sparse *Sarracenia purpurea*, a few tufts of *Eriophorum*. Some of the shrubby and arborescent species are always present as young individuals or isolated mature ones: *Nemopanthus mucronata*, *Larix laricina*, *Picea mariana*, *Acer rubrum*. This association is probably most successful after fire or following artificial drainage, or both.

* *See footnote under Chamaedaphnetum.*

Nemopanthetum mucronatae (Figs. 2, I; 3)

D s. D z c . L c*
F t d a z i. F l s a x c. M m e n f c

Nemopanthus mucronata had already appeared as isolated individuals in the *Ledetum* or the *Chamaedaphnetum*. Where it actually achieves dominance, the upper synusia (1-2 meters) which it forms can become quite dense, but mostly it will be restricted to rather less than 50% of the coverage. *Viburnum cassinoides* is usually present, also *Aronia melanocarpa* and quite often *Vaccinium corymbosum*, especially towards the terminal stage of development. A second synusia (30-60 cm.) is formed by *Ledum*, *Chamaedaphne*, *Vaccinium myrtilloides*, or *Kalmia angustifolia*. In the earliest phase of the present association, the growth of *Sphagnum* is still very strong, and can be compared to that described above in the *Chamaedaphnetum*. With the spread of the upper synusia and the consequent increase of shade at lower levels, it thins out. At that time, young *Betula populifolia* and *Acer rubrum* appear at least as scattered individuals. This association occurs only in the Lowlands, although the dominant species is also found in the Appalachians and Laurentians, and in other boreal areas.

Alnetum rugosae (Fig. 10)

D s c. D s i. H l p. L r
F t d a z c. F m d a z i. H l d v z p. M l e n f b

Alders are not usual invaders in the bog: they are more typical swamp, fen, or riparian plants, succeeding *Calamagrostis* or *Myrica*. They appear on peaty soils only on contact zones with forest, as a transitional belt. The character of the *Alnetum* in the bog sere is somewhat different to that of its other hydroseral positions, although it retains many of its associates, such as *Ilex verticillata*, and *Rhamnus alnifolia* in a second, discontinuous synusia and quite a few essentially sciophilous herbaceous plants, especially ferns; *Pteretis pensylvanica*, *Onoclea sensibilis*, *Osmunda cinnamomea*. These are typical floodplain species (*Acereto-Ulmetum laurentianum*, Dansereau (17, p. 256 and Table II). *Vaccinium corymbosum*, however, and the small tufts of *Sphagnum* at the base of the alders characterize the bog facies of the *Alnetum*. More mesic mosses are also present on the small hummocks.

Laricetum laricinae (Figs. 2, II; 12; 13)

N m i. D s r. D z r. H l c *
T m d n z i. F t d a z b. F l s a x b. H l d g z c

The larch association occurs under several facies, according to its origin. A mature stand of *Larix* is relatively rare, as larches more than 15 meters do not often form a consociation, but are usually mixed with a considerable quantity of *Picea mariana*. The typical *Laricetum*, therefore, is an open, parklike stand (50% or less coverage) with trees about 10-12 meters high, a sparse tall shrub layer (*Alnus rugosa*), an also sparse subshrub synusia

* *See footnote under Chamaedaphnetum.*

(*Ledum groenlandicum*, *Kalmia angustifolia*), and a generally quite dense sward of *Carex disperma* (Fig. 13). Very often, in fact, *Larix* and *Carex* are the only two dominants, the two intermediate synusiae being absent. Several other species are also quite frequent in the *Laricetum: Thuja occidentalis*, *Picea mariana*, *Viburnum cassinoides*, *Sarracenia purpurea* (Fig. 13), *Vaccinium myrtilloides*, *V. oxycoccos*, *Rubus pubescens*. Although *Larix* is of constant occurrence in bogs, *Laricetum laricinae* does not form in all: the conditions that allow that association to originate apparently prevail on the inner edge of the floating mat, on its hinge, so to speak. The constant height of the water-table and poor light appear to be more propitious to *Carex disperma* than to any of the *Ericaceae* (see above, under *Caricetum dispermae*).

In fact, it would seem that the *Laricetum* can invade almost any other bog association where there is enough light for the germination of larch seed (Gates (19)).

The rooting of tree species is superficial (Rigg (35, 36), Rigg and Harrar (42)), and the "soil" itself is soft, so that a strong wind overthrows them. Fallen trees accelerate the evolution of the bog by raising its level. Small water openings form between the trunks, whereas above the *Sphagnum* peat, the leaves of *Larix*, *Thuja*, and *Picea* form a coating which decomposes at an even slower rate, and is no advantage to the ecesis of bog species.

The latter, however, are favored by windfalls which brusquely increase light and permit a regression to the *Chamaedaphne* stage.

Piceetum ericaceum (Figs. 2, II, III, and IV; 4; 9; 14; 15)

E N m p. D z i. L c *

T m e n x (d n z) p. F l s a x i. M m e n f c

This association also has a parklike structure consisting of isolated but numerous individuals of *Picea mariana* or of clumps of 3 to 10 individuals (usually of different ages) rising at rather regular intervals in an otherwise even and homogeneous heath (Figs. 2, 4, 9). *Sphagnum* still forms the foundation under the heaths; in fact it grows very vigorously and competes with the subshrubs themselves in the manner indicated under *Chamaedaphnetum* and in Fig. 9. According to immediate history of development, the dominant *Ericaceae* will be *Chamaedaphne*, *Ledum*, or *Kalmia angustifolia*, very commonly a mixture of all three. Under *Picea* (and a scattering of *Larix*), the vegetation will show a more sylvatic character: the *Ericaceae* are almost entirely eliminated, and such species as *Rubus pubescens*, *Coptis groenlandica*, *Clintonia borealis*, *Maianthemum canadense*, *Dalibarda repens* will appear, and also mosses such as *Calliergonella schreberi*, *Hypnum crista-castrensis*, and even *Hylocomium splendens*. On the fringes of these islands usually persist colonies of *Carex disperma*, *Vaccinium oxycoccos*, *Eriophorum* sp.

In fact, this community has various contrasting biotopes which are illustrated in Fig. 9. Biotope *A*, the large *Sphagnum* cushion, is identical to the one that is uniformly repeated in the *Chamaedaphnetum* (Fig. 8). Biotope *B* shows a depression of the *Sphagnum* mass under either ericads or conifers.

* *See footnote, p. 513.*

In biotope *C*, enough tree growth occurs to shade the ground, and mosses other than *Sphagnum* take hold. Biotope *D* is a small island of "forest", with dense shade and a completely sylvatic flora. Microclimatic measurements have shown differences between these biotopes: *D* shows greater constancy, less variation, and less amplitude. This association, in all likelihood, will turn out to harbor the greatest number of species: it is the most heterogeneous although its four biotopes alternate regularly enough to give it apparent uniformity.

The Subclimaxes or Forest Invasion

As can be seen in Figs. 5 and 6, a distinctly new level is attained with the modification of the structure of the upper synusia: forest invasion creates conditions unfavorable to the heliophyte majority of dominants in both the early stages and the consolidation period. Most of these arborescent associations are not restricted to the bog sere, but are current subclimax types throughout their respective regions.

In the Laurentian area, *Betuletum abietosum* (as described by Dansereau (17, pp. 256-257)) comes nearest to being a bog forest; together with *Aceretum rubri* (Cain and Penfound (10)), Dansereau (17, p. 262); also Conard's (14) *Aceretum osmundaceum.*

No attempt will be made here to describe these types and to show further evolution to the Laurentian deciduous forest climax (*Aceretum saccharophori laurentianum*) as this has been done elsewhere (Dansereau (17)).

As for the Canadian forest succession, the bog term of the hydrosere culminates very closely indeed to the climax (*Piceetum marianae*), and the latter even retains some floristic elements introduced early into the succession. In other words, some climax species appear during the consolidation period and some consolidation-period species persist into the climax.*

Succession almost always takes place through a *Piceetum ericaceum* stage. The most frequent further stage is *Betuletum abietosum* and before the climax is attained, there is sometimes a long quasiclimax period of pure fir forest (*Abietetum balsameae*). The latter has few if any shrubs, but a dense ground cover of *Chiogenes hispidula* and *Linnaea borealis* var. *americana* over a continuous moss carpet where *Sphagnum* occupies the depressions, and the more mesic mosses (especially *Hylocomium splendens*) the somewhat drier biotopes.

Summary

1. The criteria used to distinguish bogs from swamps and marshes are enumerated (Table I) and discussed.

2. The dynamics of bog formation are examined and an interpretation of the processes in the Laurentian region outlined (Fig. 1).

3. The principal features of the structure of vegetation in bogs are described.

* *This interesting aspect of regional shifts in seral positions will be considered in another paper of this series.*

A recently proposed system for representing structure (Table III) is applied and brings out the differences between bog communities of equivalent successional status (Figs. 3 and 4).

4. A general scheme of seral relationships of bog communities shows their relative positions in the deciduous forest area of the St. Lawrence Lowlands (Fig. 5) and in the needle-leaf area of the Canadian Forest (Fig. 6). Three major phases are shown: pioneer, consolidation, and subclimax.

5. The most important communities in each phase are briefly described in terms of structure and composition. Küchler's system (Table II) and Dansereau's (Table III) are applied. Various figures and photographs illustrate the physiognomy of the communities.

6. Special attention is given to the ultimate synecological unit, the biotope, the smallest piece in the mosaic that composes the association. It appears that some communities have only one or two very regularly alternating biotopes, like *Chamaedaphnetum calyculatae* (Fig. 8), *Laricetum laricinae;* whilst others are much more complex like *Myricetum galeae* (Fig. 7) and *Piceetum ericaceum* (Fig. 9).

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References

1. Abbayes, H. des et Hamant, C. Répartition et comportement de *Myrica Gale* L. dans le Massif armoricain. Compt. Rend. Soc. Biogéograph. 23 (195) : 12-17. 1946.
2. Andersson, G. und Hesselman, H. Verbreitung, Ursprung, Eigenschaften und Anwendung der Mittelschwedischen Böden. 2te Intern. Agrogeologenkonf., Stockholm. 1910.
3. Auer, Vaino. Peat bogs in Southeastern Canada. Can. Dept. Mines Resources, Geol. Survey Mem. No. 162 : 1-32. 1930.
4. Baas-Becking, L. G. M. and Nicolai, E. The ecology of a sphagnum bog. Blumea, 1 : 10-44. 1934.
5. Bauman, A. und Gully, E. Die "freien Humussäuren" des Hochmoores. 1910. *Cited by* Rigg (38).
6. Bond, G. Root nodules of bog myrtle or sweet gale (*Myrica Gale* L.). Nature, 163 (4149) : 730. 1949.
7. Braun, E. L. Development of the deciduous forests of Eastern North America. Ecol. Monographs, 17 (2) : 211-219. 1947.
8. Braun, E. L. Deciduous forests of Eastern North America. Blakiston, Philadelphia, Toronto. 1950.
9. Braun-Blanquet, J. and Pavillard, J. Vocabulary of plant sociology. *Translated and published by* F. R. Bharucha, Botany School, Cambridge. Imprimerie de la Charité, Montpellier. 1930.
10. Cain, S. A. and Penfound, W. T. *Aceretum rubri:* the red maple swamp forest of Central Long Island. Am. Midland Naturalist, 19 : 390-416. 1938.
11. Carpenter, J. R. An ecological glossary. Kegan Paul, Trench, Trübner & Co., London. 1938.

12. CHOUARD, P. et PRAT, H. Note sur les tourbières du Massif de Néouvielle (Hautes-Pyrénées). Bull. Soc. botan. France, 76 : 113-130. 1929.
13. CHOUARD, P. et PRAT, H. Remarques sur l'évolution des cuvettes lacustres à propos de la pozzine et du lac de Nino. Bull. Soc. botan. France, 77 : 1-4. 1930.
14. CONARD, H. S. The plant associations of Central Long Island. A study in descriptive plant sociology. Am. Midland Naturalist, 16 : 433-516. 1935.
15. DACHNOWSKY-STOKES, A. P. Peat deposits of Ohio. Geol. Survey Ohio, Bull. 14 : 1-424. 1912.
16. DANSEREAU, PIERRE. Essai de corrélation sociologique entre les plantes supérieures et les poissons de la beine du lac St-Louis. Contribs. Inst. Biol. Univ. Montréal, 16 : 369-417. 1945.
17. DANSEREAU, PIERRE. L'érablière laurentienne. II. Les successions et leurs indicateurs. Can. J. Research, C, 24 : 235-291. 1946.
18. DANSEREAU, PIERRE. Description and recording of vegetation upon a structural basis. Ecology, 32 (2) : 172-229. 1951.
19. GATES, F. C. The bogs of Northern Lower Michigan. Ecol. Monographs, 12 (3) : 213-254. 1942.
20. GORHAM, W. C. A limnological study of certain bog lakes with special reference to the macroplankton. Unpublished doctoral dissertation, University of Michigan. 1931.
21. KÜCHLER, A. W. A physiognomic classification of vegetation. Ann. Assoc. Am. Geograph., 39 (3) : 201-210. 1949.
22. KULCZYNSKI, S. Peat bogs of Polesie. Mém. Acad. polon. Sci., Classe Sci. math. nat., B, 15 : 1-355. 1949.
23. KURZ, H. Influence of *Sphagnum* and other mosses on bog reaction. Ecology, 9 (1) : 56-69. 1928.
24. LEWIS, F. J. and DOWDING, E. S. The vegetation and retrogressive changes of peat areas ("muskegs") in Central Alberta. J. Ecol. 14 (2) : 317-341. 1926.
25. LEWIS, F. J., DOWDING, E. S., and MOSS, E. H. The vegetation of Alberta. II. The swamp, moor and bog forest of Central Alberta. J. Ecol. 16 (1) : 19-70. 1928.
26. LOBECK, A. K. Geomorphology. An introduction to the study of landscapes. McGraw-Hill Book Company, Inc., New York. 1939.
27. MARTONNE, E. de. Traité de géographie physique. II. Le relief du sol. 7e éd. Librairie Armand Colin, Paris. 1927.
28. OSVALD, H. Die Vegetation des Hochmoores Komosse. Svenska Växtosociologiska Sällskapets. Handl. 1. 1923.
29. OSVALD, H. Die Hochmoortypen Europas. Veröffentl. Geobotan. Inst. Rübel. Zürich. 1925.
30. OSVALD, H. Vegetation of the Pacific coast bogs of North America. Acta Phytogeograph. Suecica, 5 : 1-33. 1933.
31. PEARSE, A. S. Animal ecology. McGraw-Hill Book Company Inc., New York. 1939.
32. POTZGER, J. E. A notable case of bog formation. Am. Midland Naturalist, 15 (5) : 567-580. 1934.
33. POTZGER, J. E. Some acidity studies in dunes and bogs. Proc. Indiana Acad. Sci. 47 : 100-105. 1938.
34. RIGG, G. B. Physical conditions in sphagnum bogs. Botan. Gaz. 61 : 159-163. 1916.
35. RIGG, G. B. Forest succession and the growth of trees in sphagnum bogs. J. Forestry, 15 : 726-739. 1917.
36. RIGG, G. B. Growth of trees in sphagnum. Botan. Gaz. 65 (4) : 359-362. 1918.
37. RIGG, G. B. Some sphagnum bogs of the North Pacific coast of America. Ecology, 6 (3) : 260-278. 1925.
38. RIGG, G. B. The development of *Sphagnum* bogs in North America. Botan. Rev. 6 : 666-693. 1940.
39. RIGG, G. B. Comparisons of the development of some sphagnum bogs of the Atlantic coast, the interior, and the Pacific coast. Am. J. Botany, 27 (1) : 1-14. 1940.
40. RIGG, G. B. Soil and air temperatures in a sphagnum bog of the Pacific coast of North America. Am. J. Botany, 34 (9) : 462-469. 1947.
41. RIGG, G. B. The development of sphagnum bogs in North America. II. Botan. Rev. 17 (2) : 109-131. 1951.
42. RIGG, G. B. and HARRAR, E. S. The root systems of trees growing in sphagnum. Am. J. Botany, 18 : 391-397. 1931.

43. RIGG, G. B. and RICHARDSON, C. T. Profiles of some sphagnum bogs of the Pacific Coast of North America. Ecology, 19 (3) : 408-434. 1938.
44. RIGG, G. B. and STRAUSBAUGH, P. D. Some stages in the development of *Sphagnum* bogs in West Virginia. Castanea, 14 (4) : 129-148. 1949.
45. SCHIMPER, A. F. W. Plant-geography upon a physiological basis. Oxford University Press, London. 1903.
46. TARR, R. S. and MARTIN, L. College physiography. The Macmillan Company, New York. 1930.
47. TRANSEAU, E. N., SAMPSON, H. C., and TIFFANY, L. H. Textbook of botany. Harper, New York. 1940.
48. VILLAR, E. HUGUET del. Geobotanica. Edit. Labor, Barcelona, Buenos Aires. 1929.
49. WARMING, E. Oecology of plants. Oxford University Press, London. 1909.
50. WATERMAN, W. G. Ecological problems from the sphagnum bogs of Illinois. Ecology, 7 (3) : 255-272. 1926.
51. WELCH, P. S. Limnology. McGraw-Hill Book Company Inc., New York. 1935.
52. WELCH, P. S. Limnological investigations of a strongly basic bog lake surrounded by an extensive acid-forming bog mat. Papers Mich. Acad. Sci. 21 : 727-751. 1936.

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GREAT BRITAIN.